Friends of the Wild Swan
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Via e-mail to: dnrchcp@mt.gov

Dear Mr. O'Herron and Ms. Ports,

Please accept the following comments on the Final Environmental Impact Statement and
Habitat Conservation Plan for Montana DNRC's Forested Trust Lands on behalf of
Friends of the Wild Swan and Alliance for the Wild Rockies. We incorporate by
reference the comments of Defenders of Wildlife, Natural Resources Defense Council,
Montana Environmental Information Center, Audubon Society, Swan View Coalition,
Earthjustice and Stephen Braun. We also incorporate our previous comments on the
Conservation Strategies and the Draft Environmental Impact Statement because they are
still valid and relevant and were not adequately addressed in the response to comments.

The HCP does not fully minimize and mitigate to the maximum extent practicable the
"taking" of each of the covered species and their habitats, nor does it provide a net
benefit to each of the covered species, as intended by Congress. The HCP fails to
adequately prevent harm to many of the species' chances of recovery, or even their
chances of survival. The HCP also fails to take a "precautionary" approach as
recommended by the adaptive management literature.

While a few changes were made to the HCP since the DEIS they are not enough to
minimize "take" and conserve the species. The range of alternatives is unacceptably
narrow based upon what DNRC is willing to do; not what actions will contribute to the
conservation of the HCP species.

What is also missing from the FEIS and HCP is a description of the current condition of
these lands and how much take will occur from the actions sanctioned under any of the
alternatives. The FEIS is painted with rosy descriptions of how building more roads,

entering security core areas, logging in riparian areas, etc. will not have any measurable impact on the fish and wildlife covered by the HCP. However, it is contrary to best available science and the current on-the-ground condition of managed lands that these impacts will be negligible. The FEIS should detail how much loss each species will incur under the HCP. Then perhaps a true conservation alternative could be developed.

The FEIS also does not disclose how the activities sanctioned by the HCP are consistent with recovery of the listed species. There are no biological goals in the HCP only logging and roading goals. We realize that DNRC is not obligated to "recover" listed species; however, their actions should not be inconsistent with recovery.

We must again emphasize that the 50-year time period for the HCP is too long. The negative impacts from implementation of the HCP will occur in the near future while the monitoring and possible mitigation are pushed back over decades. This results in unacceptable impacts to the species the HCP is supposed to conserve.

Climate Change
The FEIS and HCP included a few more paragraphs about climate change but it is still considered a changed circumstance that will be addressed sometime in the future.

The EIS and HCP fail to account for how changes to streamside zones will result from climate change, i.e., will trees grow back at the same rate? Will trees grow back at all if they are logged in riparian areas?

Climate change will have implications for species such as bull trout because they require cold, clean water. Isaak et al (2010) state: "Riparian vegetation, for example, strongly affects near stream microclimates and minimizing near-stream disturbances associated with grazing, roadbuilding and timber harvest, or facilitating rapid vegetative recovery after these disturbances, could help buffer many streams from additional warming." (Exhibit #1)

The HCP moves in the opposite direction which could exacerbate the effects of climate change on bull trout and other cold water fishes. It allows the construction of over 1,300 miles of roads, allows logging in riparian areas and allows grazing to continue near streams.

Climate change will also increase rain on snow events resulting in stream scour. Shelburg et al's (2010) study of bull trout redd scour emphasized the importance of habitat heterogeneity and refugia availability in sustaining salmonid populations at multiple spatial scales. Loss of complex fluvial spawning habitat such as large woody debris contributes to redd scour after rain on snow events. They conclude: "Processes that form complex habitat in association with LWD may partially mitigate against unfavorable discharge regimes, water and sediment yield alterations due to land-use, or future climate change." (Exhibit #2)

The 50-foot streamside buffers in the HCP are riddled with exceptions that allow salvage logging and other activities in them thereby reducing the LWD available to the streams which can result in increased stream scour and loss of bull trout redds.

Roads

The FEIS and HCP continue to ignore the large body of scientific evidence that roads and high road densities are bad for fish, wildlife, water quality and other resources. All alternatives increase rather than decrease road densities to the same degree. Currently road densities are 3.1 linear miles/mile^2 – alternatives 1, 2 and 4 increase road densities to 4.7 linear miles/mile^2 and alternative 3 (which is supposed to include increased mitigation measures) increases the road density to 4.6 linear miles/mile^2.

This narrow range of alternatives is not consistent with the National Environmental Policy Act. Carnefix and Frissell (2001) found that 1) no truly "safe" threshold road density exists, but rather negative impacts begin to accrue and be expressed with incursion of the very first road segment; and 2) highly significant impacts (e.g., threat of extirpation of sensitive species) are already apparent at road densities on the order of 0.6 km per square km (1 mile per square mile) or less. Therefore, restoration strategies prioritized to reduce road densities in areas of high aquatic resource value from low-to-moderately-low levels to zero to low densities (e.g., <1 mile per square mile, lower if attainable) are likely to be most efficient and effective in terms of both economic cost and ecological benefit. (Exhibit #3)

The EIS describes the SFLMP ARMs as including a standard to minimize the number of road miles. Building 1,322 to 1,408 miles of new permanent roads in addition to an unquantified amount of temporary roads is not minimizing road miles by any stretch of the imagination.

In addition, the HCP must address total road densities as "take".

Another review of scientific literature on the ecological effects of roads by Trombulak and Frissell (2000) found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. (Exhibit #4)

Roads alter geomorphic processes by accelerating erosion from the road surface, affect channel structure and geometry, alter surface flows and increase sediment. They can affect site productivity by removing/displacing topsoil, altering soil properties, changing microclimate and accelerating erosion. Roads create edge and allow non-native plant species to invade forest interiors displacing native plants and decreasing forage for wildlife.

Roads increase fine sediment in streams which is linked to decreased fry emergence, decreased juvenile densities, loss of winter carrying capacity and increased predation of fishes. They are barriers to migration, increase water temperatures, and alter streamflow

regimes. Road stream crossings have negative effects on stream invertebrates reducing taxa richness.

In the Columbia River basin pools declined with increasing road density and the frequency of strong populations of salmonids declined with increasing road densities.

Roads contribute to habitat loss for terrestrial wildlife through fragmentation, edge effects, reduced densities of snags and logs. They also provide access that can lead to overhunting, overtrapping, poaching, disturbance, collisions, displacement or avoidance.

Roads can have adverse effects on biodiversity. Roads create corridors that are used by predators to more easily access the forest. Edge effects from roads contribute to nest depredation of songbirds by predators attracted to edges.

If these impacts to fish, wildlife, water quality and other resources were truly a consideration then the HCP would not allow such large increases in road densities.

Aquatic Conservation Strategies
• The HCP allows 15 years for corrective actions on high risk sediment sites in bull trout streams to be completed and 25 years for cutthroat and redband trout streams. If DNRC cannot correct problems on its existing road system for 25 years then they should not build any more roads.

• If the HCP is to benefit multiple fish species then the hierarchy for corrective actions to facilitate fish connectivity should not be tiered. Furthermore, the timeframes for correcting fish passage problems – 15 to 30 years – is too long.

• The HCP relies heavily on existing ARMs and BMPs for aquatic mitigation. If these measures were adequate then why is there a need for the HCP? The HCP must institute more stringent measures and the EIS must contain an actual range of alternatives.

• The HCP does not require that culverts be regularly monitored to ensure that they do not plug with debris and fail. It only requires that culverts be monitored for fish passage.

• The Final EIS changed the calculation of streamside buffer by removing the site-potential tree height and replacing it with tree height at 100 years. This indicates that DNRC does not plan to allow trees in riparian zones to grow more than 100 years. Over time this coupled with the riparian logging will affect stream shading and temperature.

• The Flathead Lake Biological Station has been studying the aquatic environment in the Crown of the Continent ecosystem for decades. Hauer et al (2007) found that:
> "Streams of watersheds with logging have increased nutrient loading, first as SRP and NO3, which is rapidly taken up by stream periphyton. This leads to increased algal growth that is directly correlated with the quantity of logging within the watershed. The increased periphyton increases particulate organic matter in transport as the algal biomass is sloughed into the stream. We observed this as

increased TP and TN in logged watershed streams. Other studies in the CCE have shown that increased sediment loading and an incorporation of fines into spawning gravel, especially during the summer and fall base flow period, has a dramatic effect on the success of spawning by bull trout (Salvelinus confluentus). Experiments have shown that as the percentage of fines increases from 20% to 40% there is >80% decrease in successful fry emergence." (Exhibit #5)

The increased logging and narrow stream buffers in the proposed HCP will further degrade aquatic ecosystems.

• The HCP must protect cold water temperature and maintain other stream attributes such as large woody debris. The streamside buffer was increased from 25 feet to 50 feet; however, there are still many exceptions for logging, roading and gravel mining. These include: allowing borrow pits in SMZs, allowing roads in RMZs, WMZs and avalanche chutes, allowing cable logging corridors in RMZs, allowing multiple harvest entries in RMZs and allowing salvage logging in RMZs. The narrow streamside buffer in addition to the exclusions for logging do not protect stream habitat.

• Hauer et al (1999) compared large woody debris in wilderness vs. logged watersheds in northwest Montana and concluded:

> The implications of this study for forest managers are twofold: *(i)* with riparian logging comes increased unpredictability in the frequency of size, attachment, and stability of the LWD and *(ii)* maintaining the appropriate ratios of size frequency, orientation, and bank attachment, as well as rate of delivery, storage, and transport of LWD to streams, is essential to maintaining historic LWD characteristics and dynamics. **Our data suggest that exclusion of logging from riparian zones may be necessary to maintain natural stream morphology and habitat features. Likewise, careful upland management is also necessary to prevent cumulative effects that result in altered water flow regimes and sediment delivery regimes.** While not specifically evaluated in this study, in general, it appears that patterns of upland logging space *and* time may have cumulative effects that could additionally alter the balance of LWD delivery, storage, and transport in fluvial systems. These issues will be critical for forest managers attempting to prevent future detrimental environmental change or setting restoration goals for degraded bull trout spawning streams (cf. Reeves et al. 1991). Emphasis added.

We referenced this study in our DEIS comments as a counterpoint to DNRC's conclusion that LWD recruitment would be sufficient with 25 foot buffers. This study was not used in the FEIS. It is applicable for the proposed 50 foot buffers and should be incorporated into the analysis. It is attached as exhibit #6.

• The HCP must contain a standard for sediment.

• The HCP allows localized impacts over two years without considering that these impacts can have dire effects to resident fish populations.

• The sediment reduction scheme for problem roads over 50 years does not include new road construction which skews the analysis.

Grizzly Bear
• The HCP states that a radio-collared survey of 10 grizzly bears in the Swan Valley demonstrated broad use of the valley and tolerance of high road densities. We believe this is a misinterpretation. In 2008 Chris Servheen of the USFWS stated in the Missoulian that grizzly bears in the Swan Valley had a 33% mortality rate which was unsustainable. Mr. Servheen and other bear biologists have also refuted at NCDE meetings that bears were tolerating high road densities in the Swan Valley. In fact, bears are dying in the Swan Valley, not tolerating high road densities.

• The HCP indicates that DNRC is unsure of how many roads it even has on the landscape. "If a road is encountered that is not in the transporation plan and evidence suggests that the road existed prior to the signing of the HCP DNRC will promptly notify USFWS…" If DNRC built these roads then how can they "encounter" an old road they didn't know they had? (See HCP at page 2-21)

• The HCP eliminates secure core area on the Stillwater State Forest in favor of a 4-year activity/8-year rest scheme. This should be rejected for several reasons. 1) The rest period is not a surrogate for secure core because it has many loopholes that allow salvage logging and use of closed roads by DNRC. 2) DNRC is allowed to maintain up to 8 miles of temporary roads at any one time. 3) DNRC is relying on adjacent Forest Service core area to provide grizzly bear security yet their own ARMs do not allow them to restrict their activities to make up for deficiencies on adjacent lands. They can't have it both ways. 4) The HCP characterizes adjacent Plum Creek lands as having "efforts to avoid or minimize take." However, Plum Creek does not have an HCP for grizzly bears so is not bound by any legal measures to minimize take. 5) This scheme has not proven to protect grizzly bears in the Swan Valley under the SVCA.

The HCP should include security core for grizzly bears on all blocked DNRC ownership.

• The HCP does not contain any additional measures for the grizzly bears that are listed as "endangered" in the Cabinet Yaak ecosystem.

Lynx
• The geographic scope of the HCP for lynx is inadequate.

• DNRC added a standard to maintain 20% of the lynx's winter foraging habitat and to protect 20% of the lynx's summer foraging habitat from pre-commercial thinning. But again it is riddled with exceptions such as DNRC need not maintain hare habitat where it may compete with crop trees or conflicts with its timber objectives.

• The final HCP proposes to retain just 65% of its overall lynx habitat in suitable condition, when comparable plans (Washington DNR, USFS) require retaining 70% suitable habitat.

• The CLO lynx habitat maps only have to depict suitable and temporary non-suitable lynx habitat. Apparently this is due to limitations of the SLI data for that land office. If DNRC does not have the data to map structural habitat conditions such as winter foraging habitat and summer foraging habitat the HCP should include a provision to collect it.

Monitoring and Adaptive Management
The adaptive management program lacks adequate adaptive management "triggers" and other crucial decision criteria, and does not require DNRC to take any particular action at any particular time. There is no assurance under the HCP that adaptive management will result in improvements to the HCP's conservation measures, including improvements necessary to adequately minimize or mitigate "take," ensure the species' recovery, or adjust to changing circumstances and new information.

The in-stream temperature and shade monitoring is drastically reduced after 10 years if in-stream temperatures are not showing any increase. Climate change dictates that temperature monitoring should continue for the life of the HCP. In addition, the HCP's adaptive management contains no timeframe for addressing increased temperature impacts. The HCP also hints that the quality and quantity of data that is being collected may not be adequate to develop alternative approaches. (See HCP at page 4-50.)

Similarly the monitoring for large woody debris is also reduced after 10 years if the LWD recruitment objective is met on 80% of the riparian management zone acres harvested and there is no timeframe for addressing inadequate LWD recruitment. (See HCP at page 4-49.)

Redd trampling by cattle was an issue that we raised in our FEIS comments. Rather than committing to excluding cattle from streams the HCP will complete a plan for a pilot study within 2 years and initiate a plan by year 3. It is well know that cattle in streams have multiple negative impacts to water quality and fish habitat, DNRC should ensure that cattle are removed from streams rather than studying to see if there are any effects.
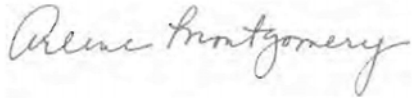
There is no mechanism to ensure that funding will be available for the monitoring of the HCP provisions by either DNRC or USFWS.

Other issues
• The HCP excludes 1,263,900 acres. DNRC should include all of its land in the HCP.

• DNRC has authorized the acquisition of thousands of acres of lands. DNRC has indicated that it may not include those lands in the HCP. These lands should be included because they provide habitat for HCP species.

• The HCP transition lands strategy states that "As soon as DNRC is aware of a proposed real estate transaction involving any HCP project area lands…notice will be provided to the USFWS…" Doesn't DNRC initiate proposed real estate transactions?

In conclusion, we do not believe that this HCP adequately minimizes and mitigates "take" of listed species and an incidental take permit should not be granted by the USFWS.

Sincerely,

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For
Michael Garrity
Executive Director, Alliance for the Wild Rockies

Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network

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Abstract. Mountain streams provide important habitats for many species, but their faunas are especially vulnerable to climate change because of ectothermic physiologies and movements that are constrained to linear networks that are easily fragmented. Effectively conserving biodiversity in these systems requires accurate downscaling of climatic trends to local habitat conditions, but downscaling is difficult in complex terrains given diverse microclimates and mediation of stream heat budgets by local conditions. We compiled a stream temperature database ($n = 780$) for a 2500-km river network in central Idaho to assess possible trends in summer temperatures and thermal habitat for two native salmonid species from 1993 to 2006. New spatial statistical models that account for network topology were parameterized with these data and explained 93% and 86% of the variation in mean stream temperatures and maximas, respectively. During our study period, basin average mean stream temperatures increased by 0.38°C (0.27°C/decade), and maximas increased by 0.48°C (0.34°C/ decade), primarily due to long-term (30–50 year) trends in air temperatures and stream flows. Radiation increases from wildfires accounted for 9% of basin-scale temperature increases, despite burning 14% of the basin. Within wildfire perimeters, however, stream temperature increases were 2–3 times greater than basin averages, and radiation gains accounted for 50% of warming. Thermal habitat for rainbow trout (*Oncorhynchus mykiss*) was minimally affected by temperature increases, except for small shifts towards higher elevations. Bull trout (*Salvelinus confluentus*), in contrast, were estimated to have lost 11–20% (8–16%/decade) of the headwater stream lengths that were cold enough for spawning and early juvenile rearing, with the largest losses occurring in the coldest habitats. Our results suggest that a warming climate has begun to affect thermal conditions in streams and that impacts to biota will be specific to both species and context. Where species are at risk, conservation actions should be guided based on considerations of restoration opportunity and future climatic effects. To refine predictions based on thermal effects, more work is needed to understand mechanisms associated with biological responses, climate effects on other habitat features, and habitat configurations that confer population resilience.

Key words: Boise River basin, Idaho, USA; bull trout; climate change; global warming; Oncorhynchus mykiss; *patch; rainbow trout;* Salvelinus confluentus; *spatial statistical model; stream temperature; thermal habitat; wildfire.*

INTRODUCTION

Environmental trends associated with a warming climate are apparent within the recent instrumental record and are projected to continue and possibly accelerate (IPCC 2007). These trends are causing distributional shifts in many thermally sensitive species as habitats move poleward or towards higher elevations (Parmesan and Yohe 2003, Root et al. 2003). The impacts of climate-induced habitat shifts may be pronounced in stream ecosystems where biota are often

ectothermic (Pörtner and Farrell 2008) and movements are constrained to linear networks that are easily fragmented by thermal or structural barriers (Fagan 2002). In streams draining the western United States, this vulnerability may be exacerbated by growing human populations with water supply needs and especially rapid climate change (Diffenbaugh et al. 2008, Saunders et al. 2008). Trends toward warmer air temperatures (Abatzoglou and Redmond 2007, IPCC 2007), increased precipitation variability (Hamlet et al. 2007), decreased snowpack (Hamlet et al. 2005, Mote et al. 2005), and increased wildfire activity (Westerling et al. 2006, Morgan et al. 2008) are already linked to warming streams and rivers (Petersen and Kitchell 2001, Morrison et al. 2002, Bartholow 2005), altered stream

hydrologies (Stewart et al. 2005, Barnett et al. 2008, Luce and Holden 2009), and increased channel disturbance from flooding and postfire landslides and debris flows (Miller et al. 2003, Istanbulluoglu et al. 2004, Hamlet and Lettenmaier 2007).

Western streams are relatively young (in geologic time), dynamic, and climatically extreme environments with limited species diversity (McPhail and Lindsey 1986, Waples et al. 2008). Salmonid fishes are most common in these environments, have broad societal importance, and are generally thought to be vulnerable to the effects of a warming climate (Keleher and Rahel 1996, Battin et al. 2007, Rieman et al. 2007). A categorical decline is not a forgone conclusion, however, because salmonids have diverse life histories and some flexibility in habitat use that confers resilience to changing environments (Quinn 2005, Crozier et al. 2008), so resolution of potential effects is important.

A growing literature links many aspects of salmonid ecology to a variety of climate-related phenomena (e.g., Mantua et al. 1997, Jager et al. 1999, Fausch et al. 2001, Mote et al. 2003, Brannon et al. 2004), but most studies have focused on thermal considerations, given the requirement of salmonids for cold temperatures (Quinn 2005, Richter and Kolmes 2005). Numerous assessments project the potential effects of increasing temperatures on habitat distributions across broad geographic domains ($>10^5$ km^2; Meisner 1990, Keleher and Rahel 1996, Nakano et al. 1996, Flebbe et al. 2006, Rieman et al. 2007) but, with few exceptions, employ air temperature–elevation relationships as surrogates for stream temperatures (Rahel 2002). This reliance on a surrogate relationship may limit the accuracy of these projections, especially at local scales and in complex terrain where adjacent streams may have very different temperature regimes (Isaak and Hubert 2001). Although broad projections will remain useful for providing strategic assessments that aid in conservation planning, more focused analyses are necessary to document actual rates of change, consider indirect effects (e.g., fire), and validate model projections.

Changes in wildfire extent and severity driven by a warming climate could have important compounding effects on thermal regimes in many western streams (Westerling et al. 2006, Falk et al. 2007). Fires that burn across small streams may cause fish mortalities from excessive temperatures (Hitt 2003), but these effects are often short-term and populations may rebound quickly through immigration from nearby refugia that were not burned (Rieman and Clayton 1997, Dunham et al. 2003b). However, fires also alter riparian vegetation and stream shade (Dwire and Kauffman 2003, Pettit and Naiman 2007), resulting in more chronic thermal effects. The importance of these effects depends on the biophysical context and severity of the fire, with some streams showing negligible responses and others heating dramatically (Minshall et al. 1997, Royer and Minshall 1997, Dunham et al. 2007). The persistence of chronic effects varies in length, with recovery occurring over a few years to several decades (Dunham et al. 2007). In certain contexts, temperature increases could become permanent if mesic prefire vegetation types such as trees fail to reestablish under climates that differ from earlier establishment periods (McKenzie et al. 2004, van Mantgem and Stephenson 2007).

Aquatic biota may respond in a variety of ways to shifting thermal conditions. At the scales of individual streams and river networks, thermally suitable habitats may expand or contract, depending on contemporary thermal regimes, the species considered, and geomorphic constraints. Where cold temperatures limit suitability in upstream areas (e.g., Nakano et al. 1996, Isaak and Hubert 2004, Coleman and Fausch 2007), warming could increase the extent of available habitats. Relatively minor temperature increases could substantially increase habitat availability given the dendritic structure of stream networks, as long as constraints associated with stream size, steepness, or anthropogenic barriers did not limit upstream movement (e.g., Rich et al. 2003, Fransen et al. 2006). In many cases, however, these constraints will exist and temperature increases are expected to reduce downstream habitats and may allow nonnative species that are broadly established in downstream areas to invade further upstream (Fausch et al. 2006, Rieman et al. 2006, Rahel and Olden 2008).

Our goal was to explore the influence of recent climate trends and wildfires on stream temperatures and thermal habitat distributions for two salmonid species with contrasting thermal tolerances. We focused on a large river network in a mountainous area of central Idaho where recent trends should be characteristic of changes in many rivers and streams across the region. Our first objective was to develop stream temperature models that accommodated important climate drivers (air temperature and stream flow), fire effects, and geomorphic factors to accurately predict stream temperatures across the network. Our second objective was to use the models to estimate changes in network-scale stream temperature patterns and thermal habitat, while also determining the relative importance of factors responsible for these changes.

METHODS

Study site

The study was conducted in the upper Boise River basin (BRB) in central Idaho, USA (Fig. 1), which is administered primarily by the US Forest Service. The BRB covers 6900 km^2 and is drained by 2500 km of fish-bearing streams ranging in elevation from 900 to 2500 m. The terrain is complex and hillslope and riparian vegetation types vary from trees to grasslands along gradients of elevation, aspect, and precipitation. Lower elevations were historically characterized by low- and mixed-severity fires with return intervals of <35 years;

return intervals for higher elevations may have been an order of magnitude longer (Brown and Smith 2000). Wildfires were relatively rare within the BRB during most of the 20th century, but have become common in the last 20 years. Approximately 14% of the BRB burned from 1993 to 2006 (our study period), but 30% burned from 1992 to 2008 (Fig. 1). Burn severity mapping conducted by the Boise National Forest suggested that areas within wildfire perimeters consisted of relatively similar proportions of high-, medium-, and low-burn severities (Dunham et al. 2007). Forest thinning activities in the northwest portion of the basin were conducted to decrease fire risk to local communities and homes in the wildland–urban interface (J. Thornton, *personal communication*).

Climate is characterized by relatively cold winters with moderate to heavy snow accumulations at higher elevations and hot, dry summers. Stream hydrographs are typical of snowmelt-driven systems in the northern Rockies, with high flows occurring from April through June and low flows during late summer and early fall. Summer thunderstorms may produce locally heavy precipitation and extreme flow events in lower order streams. Average summer air temperatures and stream flows, measured at two USGS flow gages and three NOAA weather stations in or near the basin, have been trending higher and lower, respectively (Fig. 2). These trends are consistent with regional patterns observed over the last 30–50 years (Mote et al. 2005, Stewart et al. 2005, Luce and Holden 2009).

The ichthyofauna within the BRB is relatively simple, consisting of fewer than 15 species, with headwater streams often supporting fewer than five species. We chose bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*) for study, given their conservation significance, wide distributions, well-defined and contrasting thermal preferences, and data available from previous studies (Rieman et al. 1997*a*, Dunham and Rieman 1999, Dunham et al. 2007, Neville et al. 2009). The BRB is near the southern extent of the native range for bull trout (Rieman et al. 1997*b*), but the range of rainbow trout extends much farther south (Currens et al. 2009), and the species has been widely introduced and established throughout the world (Fausch et al. 2001). Rainbow trout prefer temperatures that are several degrees warmer than bull trout (Paul and Post 2001), which have a thermal tolerance that is lower than most other freshwater fishes (Selong et al. 2001, McMahon et al. 2007). Rainbow trout spawn in both headwater and mainstem habitats. They move widely throughout life, but many populations in the BRB appear to consist primarily of resident or nonmigratory individuals (Neville et al. 2009). Rainbow trout populations in the BRB once supported an anadromous life history form, known as steelhead, but this form was extirpated from the basin with construction of downstream dams that blocked fish migrations approximately a century ago. Older bull trout may move extensively throughout larger river basins (Muhlfeld and Marotz 2005, Monnot et al. 2008), but spawning and early juvenile rearing are restricted to the coldest streams and young fish typically live in natal or associated tributary habitats for one to several years (Rieman and McIntyre 1995, Downs et al. 2006). Although bull trout remain widely distributed throughout their range, local extinctions, losses of migratory life history types, and population declines from habitat loss, overharvest, and nonnative species invasions are widely reported (Rieman et al. 1997*b*, Nelson et al. 2002). The species was listed for federal protection under the Endangered Species Act in the late 1990s (USFWS 1998) (see Plate 1).

Stream temperature database

We assembled a database of stream temperature measurements from previous studies (Rieman et al. 2006, Dunham et al. 2007) and routine monitoring efforts conducted by several natural resource agencies in the BRB (Fig. 1 and Appendix A). In 2006 and 2007, we supplemented these data with 152 observations distributed across a representative sample of small (<2350-ha contributing area), medium, and large streams (>10 000-ha contributing area) and the full range of elevations within the BRB. We also examined pre-2006 data to identify types of streams that may have been insufficiently sampled and targeted data collection in these areas to ensure representation of the widest range of conditions affecting stream temperatures.

Stream temperatures were sampled with digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy = ±0.2°C; iButton; Maxim Integrated Products, Sunnyvale, California, USA; accuracy = ±0.5°C) that recorded temperatures a minimum of five times daily (average = 72 times/d). Thermographs were placed in streams before mid-July, georeferenced, and retrieved after mid-September. This sample period encompassed the warmest portion of the year when variation in temperatures among areas is most pronounced and influence on fish growth, behavior, and distribution is potentially greatest (e.g., Scarnecchia and Bergersen 1987, Royer and Minshall 1997). Stream temperatures at other times are often near zero and relatively homothermous. Logistical constraints such as flooding and snow cover also make placement and retrieval of thermographs difficult at those times. After screening to eliminate anomalous temperature records (e.g., those downstream from reservoirs, hot springs, or beaver [*Castor canadensis*] dam complexes), 780 records at 518 unique sites were retained for analysis (Table 1). The mean summer stream temperature, defined as the period from 15 July to 15 September, and the maximum weekly maximum temperature (MWMT), which was the highest seven-day moving average of the maximum daily temperatures, were summarized from each record using
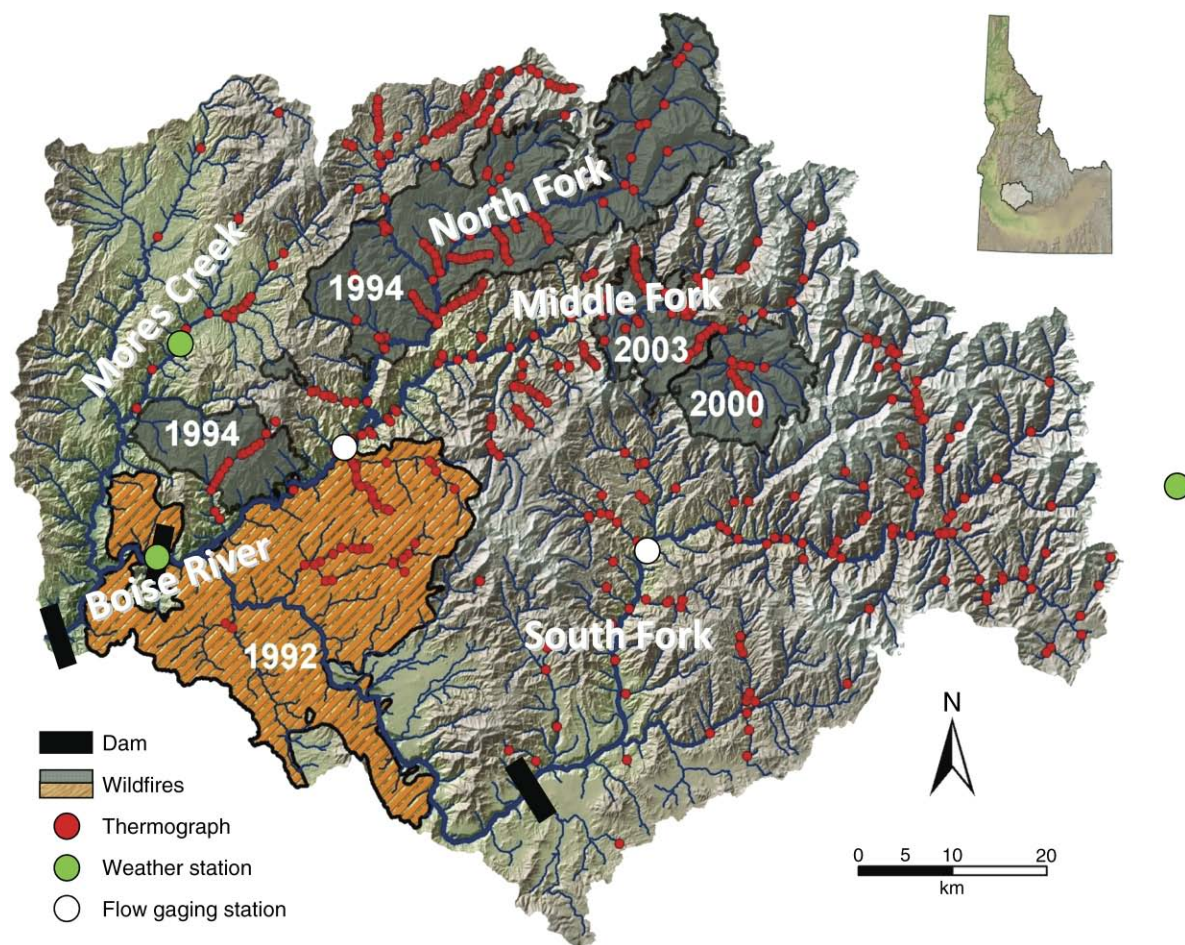
FIG. 1. The Boise River basin in central Idaho, USA. Stream temperatures were measured at 518 unique thermograph sites from 1993 to 2006 to yield 780 temperature records. Air temperatures were recorded at three weather stations, and stream flows were measured at two gages.

a SAS macro (Temperature Data Macro, *available online*).[4] The mean temperature provided a good indicator of overall thermal suitability and conditions for growth, whereas the maximum provided an indicator of transient conditions associated with seasonal extremes.

Predictor variables

We used a statistical approach incorporating predictor variables that represented important components of a stream heat budget. We developed computer scripts that ran in ArcGIS Desktop version 9.2 (Environmental Systems Research Institute, Redlands, California, USA) to quantify many of the predictors from digital map layers in a geographic information system (GIS). Values for all predictors were determined for all portions of the stream network before being matched to stream temperature records at individual locations. The syn-

[4] ⟨http://www.fs.fed.us/rm/boise/AWAE/projects/
stream_temperature.shtml⟩

thetic channel network we used was generated with TauDEM software (Tarboton 2008) using 1 arc second (30-m cell size) USGS National Elevation Dataset (NED) data as input (USGS 2006). The NED data and all predictor grids were co-registered and projected to the UTM, Zone 11, NAD 83 coordinate system.

The temperature at a point on a stream is the result of heat gains and losses that are controlled by upstream conditions (Webb et al. 2008). Conditions immediately upstream generally have greater influence than those farther away, but the extent of the spatial domains over which these conditions are most influential is unclear. Therefore, we quantified predictor variables using distance-weighted averaging for a range of domain sizes. One scheme gave all upstream cells equal weight in estimating the averaged upstream variable. The other three schemes used inverse exponential weights with *e*-folding distances (the distance at which the weight is $1/e$) of 1 km, 4 km, and 15 km. Along an individual stream this can be estimated as follows:
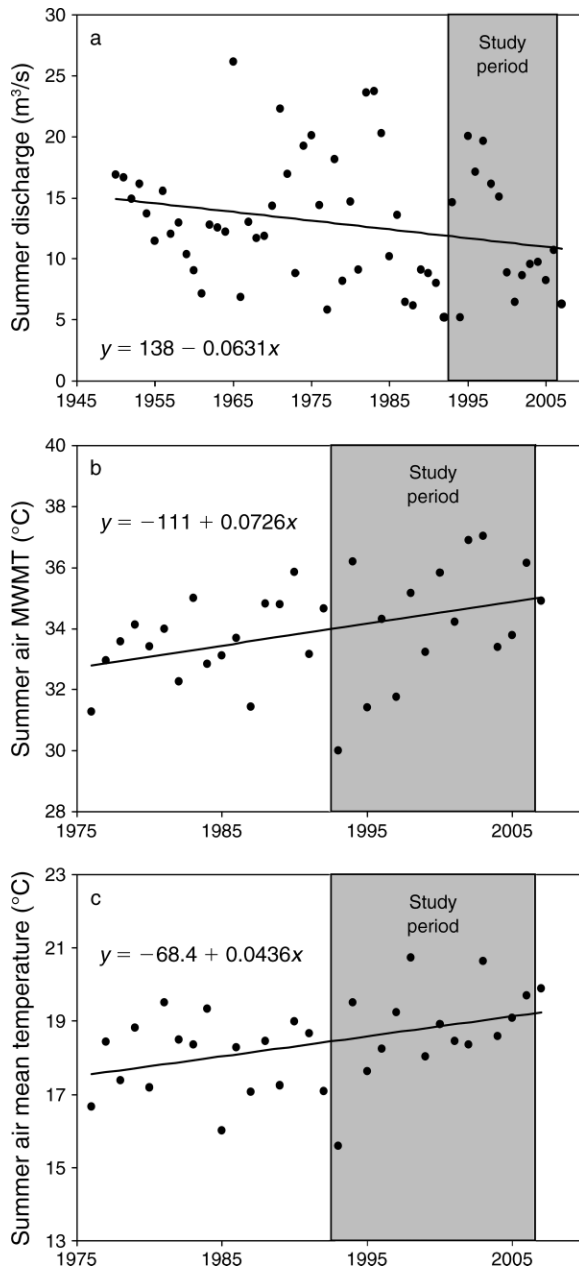
FIG. 2. Trends in (a) summer stream flow and (b, c) air temperatures in the Boise River basin. Shaded areas highlight the period for which stream temperature data were available (1993–2006). MWMT is maximum weekly maximum temperature.

$$\bar{x}_n = \frac{\sum\limits_{1}^{n} w_i x_i}{n} \quad (1)$$

where $\bar{x}_n$ is the upstream-averaged quantity at the nth cell from the upstream extent of the stream, x_i is the value of the quantity being averaged at each upstream cell, and w_i is the weight at each upstream cell. The x_i were taken from GIS coverages of the quantity of interest (e.g., elevation), and w_i is given by

$$w_i = \exp - (D_{in}/D_c) \quad (2)$$

where D_{in} is the distance between the nth and ith cell along the stream path (using simple eight-direction flow vectors between cells) and D_c is the e-folding distance (i.e., 1 km, 4 km, or 15 km). While Eq. 1 is written as if along one flow line, it can be expanded to encompass any set of contributing cells, including flow lines that include tributaries or every cell within a contributing basin. Final calculations were made using two accumulation routines: (1) network accumulation, in which data were summarized only along cells in stream channels (extracted from the DEM using TauDEM), and (2) catchment accumulation, in which data were summarized using the entire catchment area that drained to a cell on the stream network. For each variable, the averaging method that provided the strongest bivariate correlation with stream temperature was retained for use in temperature model development.

Geomorphic predictors.—Predictors in this category represented relatively static features of the river network, valley bottoms, and upstream watersheds that were hypothesized to affect stream temperatures. Six geomorphic predictors were summarized, including: watershed contributing area (C_A), network drainage density (D_D), elevation (Ele), valley glaciation (G_V), channel slope (SL), and alluviated valley bottom extent (V_B). Table 2 provides additional measurement details and summarizes the rationale for inclusion of the predictor variable and its correlation with stream MWMT across various distances. The strongest correlations generally occurred at shorter distances (1–4 km), suggesting that geomorphic influences on stream heating were relatively localized phenomena. Similar results were observed for mean stream temperature and are not reported.

Solar radiation predictor.—Solar radiation is a primary factor in stream heat budgets (Johnson 2003, Caissie 2006) that can change dramatically when fires burn through riparian areas. To quantify these effects, we used Thematic Mapper (TM) satellite imagery classifications of riparian vegetation linked to field measurements of radiation at the stream surface. Complete imagery sets for the BRB were available for 10 July 2002 (Landsat 7 ETM+) and 14 July 1989 (Landsat 5 TM), which encompassed the majority of wildfire-related vegetation changes during our study period. Classifications were done within a buffer of two grid cells along each bank (120 m total width) of the synthetic stream network. An initial classification signature set was rendered using the ISODATA algorithm (Tou and Gonzalez 1974) and 1-m National Agricultural Imagery Program (NAIP) photography was used to prune high-variance signatures. The remaining set was then input to a maximum-likelihood

TABLE 1. Descriptive statistics for variables in a data set used to build stream temperature models for the Boise River basin, Idaho, USA.

Variable	n	Mean	Median	SD	Minimum	Maximum
C_A (ha)	518	6852	1423	24 148	20	263 131
D_D (km/km^2)	518	1.22	1.21	0.27	0.08	2.14
Ele (m)	518	1799	1791	278	1095	2528
G_V (%)	518	11.0	0.0	25.0	0.0	100.0
SL (%)	518	11.5	10.9	4.4	2.5	29.0
V_B (%)	518	11.7	0.0	19.5	0.0	92.7
Rad ($\mu J \cdot m^{-2} \cdot yr^{-1}$)	518	402	403	74	151	654
Air MWMT (°C)	14	34.2	34.3	2.15	30.0	37.0
Air mean (°C)	14	18.8	18.7	1.29	15.6	20.7
Flow (m^3/s)	14	12.1	10.2	4.8	5.2	20.0
Stream mean (°C)	780	11.9	11.7	2.7	5.4	21.8
Stream MWMT (°C)	780	17.2	16.9	4.2	7.2	30.7

Notes: Variable abbreviations are: C_A, watershed contributing area; D_D, drainage density; Ele, mean basin elevation; G_V, glaciated valley; SL, channel slope; V_B, alluviated valley bottom; Rad, total direct and diffuse incoming radiation; air MWMT, maximum weekly maximum air temperature; air mean, mean air temperature from 15 July to 15 September; flow mean, mean stream flow from 15 July to 15 September; stream mean, mean stream temperature from 15 July to 15 September; stream MWMT, maximum weekly maximum stream temperature.

classifier (Leica Geosystems 2006) to derive final classifications of open, shrub, conifer, or water.

Final classifications were validated by comparison to those made at 158 random points by an independent analyst using the NAIP photography. Overall classification concordance was 80%, with agreement rates of 82% in open areas, 65% in shrub, 90% in conifer, and 82% for water. Additionally, comparisons of vegetation differences between 1989 and 2002 imagery sets confirmed the expected patterns, with vegetation inside fire perimeters trending toward more open riparian conditions (vegetative loss [e.g., tree to open] = 32.6% of cells, gain = 5.13% of cells; Appendices B and C). It was also most common for cells classified as trees to shift to open categories (70.6%). Changes outside fire perimeters also occurred, but tended to offset (gain = 12.5%; loss = 11.3%) and be spatially distributed rather than clustered.

Solar radiation was estimated using hemispherical canopy photography at 181 field sites in 2003. Field sites were visited in June and distributed among a range of riparian vegetation types and stream sizes (C_A = 135–3000 ha). Photographs were acquired using a fish-eye lens and panchromatic film with the camera mounted on a tripod at midstream 1 m above the water surface. The film was analyzed using Hemiview software (Dynamax, Houston, Texas, USA) to estimate total (direct and diffuse) radiation. These values were associated with the vegetation classification cells along the synthetic stream network, and simple power-law relationships were constructed that predicted total radiation from vegetation type and watershed contributing area (Appendix D). Upper radiation limits were imposed at 1000 $\mu J \cdot m^{-2} \cdot yr^{-1}$ to approximate the level at which riparian vegetation would no longer significantly shade large streams. These relationships conformed to general expectations, with radiation levels being higher for open/shrub vegetation classes than for trees and increasing with watershed size (stream width).

Radiation values for all remaining cells within the stream network were predicted using these relationships.

Radiation values for years between 1989 and 2002 were calculated by interpolating vegetation classifications and applying the power-law relationships. Interpolations within fire perimeters were made by assuming that losses of vegetation (i.e., tree to shrub, tree to open, or shrub to open) between the two imagery sets occurred in association with the fire. One fire occurred in 2003 after our last TM imagery set. In this instance, radiation values were estimated using fire severity map classifications (high, medium, low, none) as surrogates for vegetation change and assuming that radiation estimates from hemispherical photographs in burned areas were representative of other areas with similar burn severities. Once radiation values were assembled for all years in the study period, this predictor variable was also quantified across several spatial domains, as was the case with geomorphic predictors, to determine the strongest correlation with stream temperature (Table 2).

Climate predictors.—Interannual variation in climatically influenced factors such as air temperature and stream flow have important consequences for stream temperatures. Air temperature affects stream temperature through sensible heat exchange near the surface of the stream and by influencing temperatures of near-surface groundwater, which is an important component of summer flows. Stream flow determines the volume of water available for heating; larger flows have greater thermal capacities and are less responsive to heating (Hockey et al. 1982, Caissie 2006). We used annual summer summaries of each variable to represent interannual differences, or a year effect, common to all observations. Measures of air temperature were derived from time series of average daily temperatures obtained from three NOAA weather stations that are operated in or near the basin (Arrowrock, Idaho City, and Ketchum

TABLE 2. Geomorphic and radiation variables used to predict stream temperatures.

Variable	Rationale	References	Accumulation routine	Correlation with stream temperature			
				1 km	4 km	15 km	Upstream
C_A	Contributing area is a surrogate for stream size. Larger streams have been exposed to insolation over a greater length and are less shaded by adjacent riparian vegetation.	Moore et al. (2005), Brown and Hannah (2008)	watershed channel	··· ···	··· ···	··· ···	**0.29** ···
D_D	Drainage density is an indicator of the amount of stream exposed to solar radiation. Higher drainage densities are expected to warm stream temperatures.	Johnson (2003), Caissie (2006), Brown and Hannah (2008)	watershed channel	··· **0.30**	··· 0.29	··· 0.26	··· 0.24
Ele	Cooler air temperatures and greater snow accumulations (cooler groundwater inputs) at higher elevations should negatively affect stream temperatures.	Smith and Lavis (1975), Meisner et al. (1988), Sinokrot and Stefan (1993)	watershed channel	-0.60 -0.59	-0.57 -0.57	-0.50 -0.50	-0.43 -0.44
G_V	Glaciated valleys should cool stream temperatures because these valleys accumulate heavy snowfall and glacial detritus acts as an aquifer that stores and releases cold water during summer.	Brown et al. (2007), Brown and Hannah (2008)	watershed channel	-0.33 ···	$-\mathbf{0.39}$ ···	-0.37 ···	-0.34 ···
SL	Channel slope affects flow velocity and equilibration time to local heating conditions. Steeper slopes and greater velocities should negatively affect stream temperatures because conditions farther upstream at higher elevations have greater influence on local temperatures.	Donato (2002), Sloat et al. (2005), Webb et al. (2008)	watershed channel	··· $-\mathbf{0.29}$	··· -0.26	··· -0.25	··· -0.23
V_B	Alluviated valley bottoms act as aquifers to enhance hyporheic recharge and cool stream temperatures.	Poole and Berman (2001), Burkholder et al. (2008)	watershed channel	··· **0.17**	··· 0.14	··· 0.10	··· 0.10
Rad	Solar radiation is a major factor in stream heat budgets and should increase stream temperature.	Johnson (2003), Caissie (2006)	watershed channel	··· 0.41	··· **0.46**	··· 0.46	··· 0.46

Notes: Reported correlations were with maximum weekly maximum temperature (MWMT); values in boldface indicate upstream distance associated with predictor used in stream temperature models. C_A was calculated by accumulating the number of upslope grid cells that contributed to a cell on the synthetic stream network; D_D was computed by dividing the contributing area for a grid cell into the upstream channel length; Ele was the average for grid cells within a contributing area or cells on the stream network; G_V was estimated as a percentage of C_A after identifying glaciated valleys on a digital elevation model (DEM); SL was calculated as change in elevation per length between stream confluences; V_B was estimated as a percentage of C_A using an ArcGIS script that delineated flat, unconfined areas adjacent to the stream network. Accumulation routine was measured along the upstream channel network or watershed contributing area. Ellipses (...) indicate that the calculations were not made.

stations; Fig. 1). These data were strongly correlated ($r = 0.74–0.91$), so the individual time series were averaged and the same summary metrics that were applied to stream temperatures were applied here (i.e., summer mean and MWMT). Flow data were obtained from two USGS stream gages in the basin (Twin Springs and Featherville gages; Fig. 1). These two sets of data were also strongly correlated ($r = 0.97$) and were averaged to calculate annual mean flow from 15 July to 15 September.

Stream temperature models

Climatic influences on stream temperatures are often assessed using mechanistic models (Caissie 2006), but data requirements limit their utility in remote areas and in smaller streams where microclimates associated with riparian vegetation strongly affect local heat budgets. Statistical models, though correlative, require less parameterization of physical constants, provide estimates of parameter precision, and can be applied across a range of spatial scales when linked to a GIS. Therefore, we used multiple regressions to model the relationship between our stream temperature observations and predictor variables. Because our temperature observations came from multiple sources and were collected using a variety of sampling designs, the data could not be considered random. Fitting these data with a model that did not account for spatial structure could produce biased parameter estimates and autocorrelated error structures (Legendre 1993). To circumvent these problems, we applied recently developed spatial statistical models that account for the unique forms of spatial dependence (e.g., longitudinal connectivity, flow volume, and flow direction) inherent to stream networks

(Peterson and Ver Hoef 2010, Ver Hoef and Peterson 2010). Previous applications of these models suggest they provide valid covariance structures for streams and yield significantly improved predictive power when spatial autocorrelation is present in stream data (Peterson et al. 2006, 2007).

Because patterns in stream temperature are spatially complex, we used a stream network model with a mixed-model error structure developed by Ver Hoef and Peterson (2010). The mixed model is essentially a variance component approach, which allows multiple covariance matrices to be combined to provide a robust and flexible covariance structure. Here, covariances based on Euclidean distance are combined with "tail-up" and "tail-down" covariances. Tail-up covariances are based on hydrologic distance, but restrict spatial correlation to "flow-connected" sites (water must flow downstream from one site to another). In addition, spatial weights are incorporated to account for the disproportionate effects that tributaries of differing size may have on downstream areas. Tail-down covariances allow spatial correlation between any two "flow-unconnected" sites, meaning that they reside on the same network (share a common outlet downstream). The mixed models were fit using three covariance component models; the exponential tail-up, the exponential Euclidean, and the linear-with-sill tail-down components. The exponential tail-up autocovariance between flow-connected locations on the stream network is

$$C_{TU}(s_i, s_j \mid \theta)$$

$$= \begin{cases} 0 & \text{if } s_i \text{ and } s_j \text{ are flow-unconnected} \\ \prod_{k \in B_{s_i s_j}} \sqrt{w_k} C_1(h \mid \theta) & \text{if } s_i \text{ and } s_j \text{ are flow-connected} \end{cases}$$

$$(3)$$

where

$$C_1(h \mid \theta) = \sigma_{TU}^2 \exp\left(\frac{-h}{\alpha}\right).$$

Here,

$$\prod_{k \in B_{s_i s_j}} \sqrt{w_k}$$

represents the spatial weights, h is the total hydrologic distance between locations s_i and s_j, and θ is the parameter vector containing $\sigma_{TU}^2 > 0$ (the tail-up partial sill or variance component in the mixed model) and $\alpha > 0$ (the spatial range parameter). Also note that $C_1(h \mid \theta)$ is an unweighted exponential autocovariance function. When used in the tail-up model, it is not guaranteed to produce a valid covariance matrix until it has been weighted appropriately using the spatial weights matrix (Ver Hoef et al. 2006). However, if h in $C_1(h \mid \theta)$ were to be replaced with Euclidean distance, there would be no need for weighting and the product would be a valid

exponential Euclidean distance matrix (Cressie 1993). The linear-with-sill tail-down autocovariance function represents both flow-connected and flow-unconnected locations and is constructed as follows:

$$C_{TD}(s_i, s_j \mid \theta) = \begin{cases} \sigma_{TD}^2 \left(1 - \frac{\max(a,b)}{\alpha}\right) I\left(\frac{\max(a,b)}{\alpha} \leq 1\right) \\ \qquad \text{if } s_i \text{ and } s_j \text{ are flow-unconnected} \\ \sigma_{TD}^2 \left(1 - \frac{h}{\alpha}\right) I\left(\frac{h}{\alpha} \leq 1\right) \\ \qquad \text{if } s_i \text{ and } s_j \text{ are flow-connected} \end{cases}$$

$$(4)$$

where a and b represent the hydrologic distance from sites s_i and s_j to the nearest common downstream confluence between the two locations, θ is the parameter vector containing $\sigma_{TD}^2 > 0$ (the tail-down partial sill or variance component in the mixed model) and $\alpha > 0$ (the spatial range parameter), and $I(\cdot)$ is the indicator function.

The data to run the spatial models included the temperature observations, predictor variables, x, y coordinates for each location, a matrix containing the hydrologic distance between all sites (both predicted and observed), and a spatial weights matrix. The hydrologic distances and spatial weights were calculated in ArcGIS using customized scripts and the functional linkage of water basins and streams (FLoWS) toolset (Theobald et al. 2006, Peterson et al. 2007). These matrices were computed from the TauDEM vector stream network to ensure alignment with each of the predictor variable grids used in the study. The spatial weights were based on watershed contributing area, which was used as a surrogate for stream size and discharge.

Our stream temperature data set contained sites that were sampled in multiple years, but the spatial statistical models we employed were not true space–time models. To accommodate the temporal dimension of our data, we adjusted the location of repeat observations slightly upstream or downstream (<100 m) from the original site location to create small nonzero distances. These observations retained the same set of geomorphic predictors associated with the original site, but were assigned different sets of air temperature, stream flow, and radiation values based on their respective year. This adjustment effectively translated temporal variation to the climatic and radiation variables that were of primary interest and treated the climate variables as class variables affecting all sites similarly within a given year.

To determine which fixed effects would constitute the best stream temperature models, a set of a priori candidate models was developed. This set included a simple "elevation-only" model, a global model with all predictors, the global model with significant interactions, and several reduced forms that combined different subsets of predictors (e.g., geomorphic predictors, climate predictors, etc.). To provide a reference point

for the spatial model results, we also parameterized these candidate models using traditional, nonspatial regression methods. All parameters were derived using maximum-likelihood estimation. Standard diagnostic tests were performed, including checks for residual normality and calculation of variance inflation factors (VIFs) to assess potential problems with multicollinearity (Helsel and Hirsch 1992).

For model comparisons, we calculated spatial Akaike information criterion (AIC) values (Hoeting et al. 2006), which are similar to standard AIC, but penalize models for the number of parameters used to estimate the autocovariance structure. Although information theoretic procedures such as AIC have rapidly become the norm in many model selection contexts (Burnham and Anderson 2002), models used for bioclimatic predictions are often criticized for insufficient spatial and temporal validation (Dormann 2007). To minimize these concerns, we split our data into a training set used for preliminary model fits ($n = 728$) and a validation set composed of temperature observations that were spatially isolated from other sites ($n = 52$). In earlier spatial analyses of stream temperature data, distances of 5–15 km were reported between spatially independent sites (Gardner et al. 2003, Peterson et al. 2006), so we exceeded this distance when selecting observations for the spatial validation data.

Models were fit using the training data, and the universal kriging algorithm (Cressie 1993) was used to predict temperatures at validation sites in the spatial models. Predictive accuracy was assessed by calculating the squared Pearson correlation coefficient (r^2) between predicted and observed values. Leave-one-out cross-validation predictions were also generated using the training data for each model and used to calculate the root mean square prediction error (RMSPE). After the models with the best set of fixed effects were identified, the models were refit to the pooled set of observations from the training and validation sets.

Stream temperature predictions

Final models were used to make stream temperature predictions at both the basin scale and within burned areas by adjusting input values for air temperature, flow, and radiation to match the "average" set of conditions at the beginning and end of the study period. The radiation values used were from 1993 and 2006. Average stream flow values for these years were derived from a regression of flow on year for the 56-year period from 1950 to 2006 (Fig. 2). Air temperature values were derived similarly, but using a shorter, 30-year period from 1976 to 2006 to accommodate warming rates that are accelerating through time (IPCC 2007). Climate data were obtained from the same air temperature and flow stations described above (see *Methods: Climate predictors*) and regressions were based on averages across stations. The rates of change described by the regressions were comparable to recent global circulation

model (GCM) projections for the Pacific Northwest (Mote et al. 2008).

To determine the relative importance of the three dynamic predictors in any stream temperature changes that occurred during the study period, we also predicted temperatures by holding input values for two predictors at their 1993 values and changing the value of the third predictor between its 1993 and 2006 values. The process was repeated for each of the predictors and the stream temperature change associated with each predictor was divided by the total basin scale stream temperature change (or total burned area stream temperature change) that occurred between 1993 and 2006, as described in the previous paragraph.

After setting the input values for the various comparisons, temperature predictions were made using the universal kriging algorithm at 2487 points spaced at 1-km intervals throughout that portion of the stream network where contributing areas exceeded 400 ha. Smaller contributing areas rarely support streams wider than 2 m in this region, which appears to be a minimum for providing the necessary perennial flow and habitat volume to support a resident fish population (Dunham and Rieman 1999, Rich et al. 2003).

Effects on thermal habitat

Basin-scale maps of predicted stream temperatures were converted to thermally suitable habitats for each species by applying different temperature criteria. These criteria were derived from field samples of fish densities at 249 sites on 20 central Idaho streams conducted in 2007 (Appendix E). We considered suitable thermal habitats to be those in which each species occurred regularly and high-quality habitats to be those temperatures with the highest densities of individuals. For bull trout, we further refined these criteria by focusing on the distribution of juveniles (<150 mm) that are indicative of spawning and rearing habitats (Rieman and McIntyre 1995, Dunham and Rieman 1999). This targeted our analysis on a critical subset of habitats required for bull trout population persistence and should have provided a more precise climatic assessment for this species. Portions of the stream network with MWMT < 17.5°C (means < 12°C) were considered to be suitable habitat for bull trout, whereas high-quality habitats were defined where MWMTs were <15°C (means < 10°C). Similar precision in defining thermal habitats for rainbow trout was not possible because juveniles are more widely distributed. So instead we relied on the occurrence of fish of all ages and areas with MWMT > 15°C and < 20°C (mean > 11°C and <14°C) were considered high-quality habitats and areas with MWMTs > 12.5°C (means > 9°C) were considered suitable habitats. We did not define an upper temperature limit for rainbow trout habitat suitability because it appears to be warmer than the temperatures regularly observed in the Boise (McCullough et al. 2001, Dunham et al. 2007). With this exception, our temperature

TABLE 3. Summary statistics for candidate multiple regression models used to predict stream maximum weekly maximum temperature (MWMT).

Model description	Fixed effects	Model type	p	ΔAIC	Training data ($n = 728$)		Validation data ($n = 52$)	
					r^2	RMSPE	r^2	RMSPE
1) Global + interactions	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A, C_A × Rad, Air_MWMT × Rad, Air × Flow, Ele × G_V	spatial	20	0	0.880	1.41	0.476	2.85
2) Global	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A	spatial	16	35	0.878	1.42	0.545	2.66
3) Simple hybrid	**Ele, Rad, Air_MWMT, Flow**	**spatial**	**12**	**51**	**0.874**	**1.45**	**0.612**	**2.51**
4) Dynamic predictors	Rad, Air_MWMT, Flow	spatial	11	77	0.870	1.47	0.468	2.84
5) Geomorphic predictors	Ele, G_V, V_B, SL, C_A	spatial	13	204	0.849	1.58	0.511	2.71
6) Elevation	Ele	spatial	9	222	0.845	1.60	0.560	2.57
7) Global + interactions	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A, C_A × Rad, Air_MWMT × Rad, Air × Flow, Ele × G_V	nonspatial	13	768	0.586	2.62	0.369	3.12
8) Global	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A	nonspatial	9	808	0.562	2.70	0.428	2.98
9) Simple hybrid	**Ele, Rad, Air_MWMT, Flow**	**nonspatial**	**5**	**838**	**0.542**	**2.76**	**0.495**	**2.78**
10) Geomorphic predictors	Ele, G_V, V_B, SL, C_A	nonspatial	6	955	0.463	2.99	0.318	3.31
11) Elevation	Ele	nonspatial	2	1023	0.408	3.13	0.288	3.37
12) Dynamic predictors	Rad, Air_MWMT, Flow	nonspatial	4	1137	0.308	3.39	0.130	3.63

Notes: Models are ordered based on Akaike information criterion (AIC) values; p is the number of parameters. Final models are in boldface. RMSPE is root mean square prediction error. See Table 2 for explanations of variable abbreviations.

criteria were generally consistent with others reported in the literature for these species (Bjornn and Reiser 1991, Ebersole et al. 2001, McCullough et al. 2001, Dunham et al. 2003a, Isaak et al. 2009).

Areas meeting these criteria were summarized based on the absolute amount of habitat, as well as the number and size of discrete habitat areas or "patches" (i.e., a continuous network of thermally suitable habitat). The size of individual habitat patches appears to be particularly relevant to persistence in many salmonid species (Isaak et al. 2007, Dunham et al. 2008). Larger patches tend to support larger populations that are less susceptible to extirpations through small population effects and probably contain a greater diversity of habitats to provide resilience against environmental stochasticity (White and Pickett 1985, Sedell et al. 1990). Previous studies with bull trout in the BRB support this notion, suggesting patches > 3000 ha (~10 stream km) have a 50% probability of occupancy, whereas patches > 10 000 ha (~40 stream km) have a 90% probability of occupancy (Rieman and McIntyre 1995, Dunham and Rieman 1999).

RESULTS

The stream temperature database encompassed substantial interannual variation in climatic and solar radiation conditions across a diversity of local geomorphologies and streams (Table 1; Fig. 2). Observed mean stream temperatures ranged from 5.4° to 21.8°C (mean = 11.9°C) and MWMTs ranged from 7.2° to 30.7°C (mean = 17.2°C). Correlations among predictor variables were not particularly strong, with the exception of the two air temperature measures. Stream temperature was most strongly correlated with elevation, but also had moderate correlations with radiation and several other factors (Appendix F).

Stream temperature models

Summary statistics for candidate models predicting stream MWMT are provided in Table 3. Spatial models, despite having larger numbers of parameters, significantly outperformed their nonspatial counterparts, as indicated by lower RMSPE and AIC values, and greater predictive ability with training data (spatial $r^2 \sim 0.87$ vs. nonspatial $r^2 \sim 0.55$). Spatial models also performed better than the nonspatial models at the validation sites, although the differences were smaller. The highest AIC ranking was for a spatial model that included all predictor variables and four interactions. When applied to validation data, however, this model had poorer predictive ability than several others. Because we wanted a model that best predicted stream temperatures across the BRB, we chose a simpler model (eight fewer parameters) that performed best with the validation data ($r^2 = 0.61$) and retained good predictive ability with training data ($r^2 = 0.87$). This model included predictors for elevation, radiation, air MWMT, and stream flow. Results for mean stream temperature models were similar and are not shown.

Parameter estimates and summary statistics for the spatial and nonspatial versions of the final temperature models based on the reconstituted database are summarized in Table 4. The RMSPE for the spatial MWMT model was 1.54°C, a significant improvement over 2.75°C for the nonspatial model. Approximately two-thirds of the variance explained in the spatial MWMT

TABLE 4. Parameter estimates and summary statistics for nonspatial and spatial parameterizations of final stream temperature models (all $P < 0.001$).

Predictor	b (SE)	t	r^2	RMSPE	Variance component	
					Fixed effect (%)	Spatial error (%)
MWMT						
Spatial						
Intercept	14.3 (2.45)	5.86	0.857	1.54	62.8	37.2
Elevation	−0.00573 (0.000789)	−7.27				
Radiation	0.0156 (0.00201)	7.78				
MWMT air	0.234 (0.0353)	6.61				
Mean flow	−0.125 (0.0209)	−5.98				
Nonspatial						
Intercept	18.8 (2.61)	7.19	0.543	2.75	100	...
Elevation	−0.00795 (0.000385)	−20.7				
Radiation	0.0189 (0.00138)	13.8				
MWMT air	0.212 (0.0625)	3.38				
Mean flow	−0.255 (0.0355)	−7.19				
Mean						
Spatial						
Intercept	8.20 (1.23)	6.64	0.925	0.736	72.3	27.7
Elevation	−0.00447 (0.000438)	−10.2				
Radiation	0.00850 (0.00108)	7.90				
Mean air	0.479 (0.0225)	21.3				
Mean flow	−0.111 (0.00878)	−12.7				
Nonspatial						
Intercept	13.3 (1.23)	10.8	0.679	1.53	100	...
Elevation	−0.00637 (0.000216)	−29.5				
Radiation	0.0104 (0.000765)	13.6				
Mean air	0.392 (0.0549)	7.14				
Mean flow	−0.173 (0.0176)	−9.85				

Notes: RMSPE is root mean square prediction error. MWMT is maximum weekly maximum temperature.

model could be attributed to fixed effects and one-third to spatial structure in model residuals. All parameter estimates were significantly different from zero ($P < 0.001$) and their signs were in agreement with the expected influence. Contrasts between the spatial and nonspatial versions of the mean temperature model were similar to those associated with the MWMT models, but the mean stream temperature models predicted this metric more accurately and a larger proportion of explained variation was attributable to the fixed effects. Scatter plots of predictions from the final models vs. observed temperatures confirmed the improved accuracy of the spatial models relative to the nonspatial models (Fig. 3), but a slight bias towards over- (under-) predictions in the coldest (warmest) streams remained. Additional details regarding the final spatial models are given in Appendices G and H, including the relative contributions of each covariance type in the mixed-model structure and empirical semi-variograms that describe spatial trends in model residuals.

Stream temperature and habitat predictions

The difference between basin-scale stream temperatures predicted at the beginning and end of the study period suggest that mean summer stream temperatures increased by 0.38°C (0.27°C/decade) and MWMTs increased by 0.48°C (0.34°C/decade); Figs. 4 and 5). These temperature increases correlated most strongly with trends in air temperature and secondarily with stream flow. Radiation increases, primarily associated with the wildfires that burned 14% of the basin, accounted for ~9% of basin-scale warming. Within wildfire perimeters, however, temperature increases were 2–3 times greater than the basin averages and radiation gains played a much larger role, accounting for 50% of total stream warming. Maps of the 1993–2006 mean stream temperature changes indicated that all portions of the BRB network warmed, with the smallest increases occurring in the southern half of the basin and the largest increases within wildfire perimeters (Fig. 5). Larger-than-average temperature increases were also observed in the northwest portion of the basin outside fire perimeters, probably in response to forest thinning activities.

Stream temperature increases had different effects on thermal habitat for bull trout and rainbow trout. Rainbow trout habitats encompassed much of the stream network in 1993 and the total amount of estimated habitat was not substantially affected by warming trends (Table 5, Fig. 6). The most notable changes were small habitat gains at higher elevations (sometimes accelerated within wildfire perimeters) as unsuitably cold areas became thermally suitable. Bull trout natal habitats, in contrast, initially encompassed approximately half the BRB stream network and experienced systematic declines because these areas
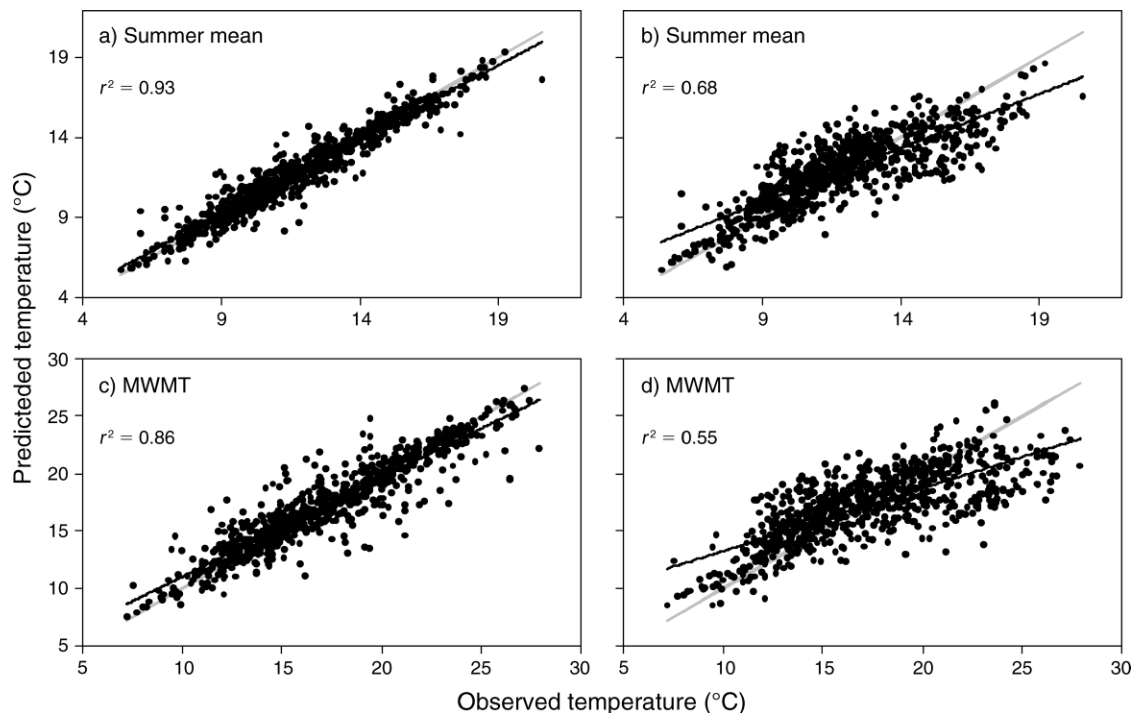
FIG. 3. Scatter plots of stream temperatures predicted from the (a, c) final spatial and (b, d) nonspatial models vs. observed values. The gray line indicates a 1:1 relationship; the black line is the simple linear regression between predicted and observed. MWMT is maximum weekly maximum temperature.

already occurred at the upper terminus of the network and losses in low-elevation sites were not offset by gains farther upstream (Table 5, Fig. 6). The total length of thermally suitable stream based on mean temperature criteria decreased by 11–20% (8–16%/decade), and the size of remaining natal patches was reduced by 10–18%. The greatest reductions occurred within wildfire perimeters and for the coldest, high-quality habitats because these areas comprised a smaller area at the outset of the study and changes relative to this baseline were amplified.

Discussion

Our results suggest that environmental trends associated with a warming climate have begun to alter temperatures and thermal habitat distributions in streams across the BRB. Given the geographic breadth of recent wildfires (Westerling et al. 2006, Morgan et al. 2008), air temperature increases (Mote et al. 2005, Abatzoglou and Redmond 2007), and summer stream flow decreases (Stewart et al. 2005, Luce and Holden 2009) across much of the western United States, we believe similar thermal alterations are likely in many river networks. Whether these alterations have significant biological implications ultimately depends on local conditions. For a relatively mobile species such as rainbow trout, which has widely distributed and well-connected habitats in the BRB, the effects may be relatively benign. With some exceptions associated with

structural barriers, rainbow trout populations should be able to track upstream shifts in habitat. Moreover, the wildfires associated with climate change may increase stream productivity, the availability of important forage
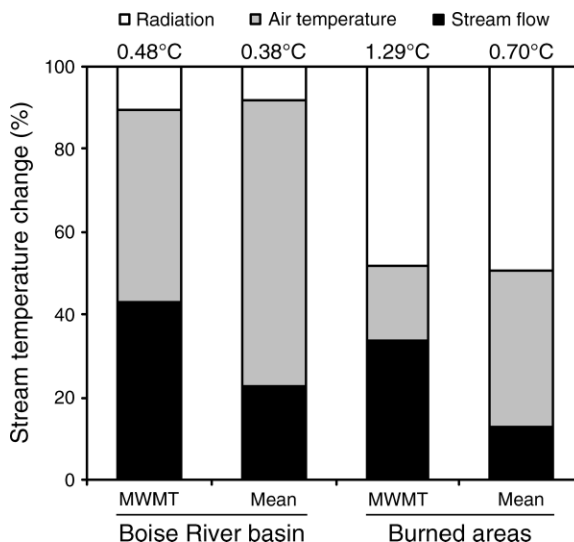

FIG. 4. Percentage of stream temperature change from 1993 to 2006 within burned areas and across the Boise River basin that was attributable to radiation gains associated with fires and long-term trends in air temperature and stream flow. Values above bars are total stream temperature increases. MWMT is maximum weekly maximum temperature.
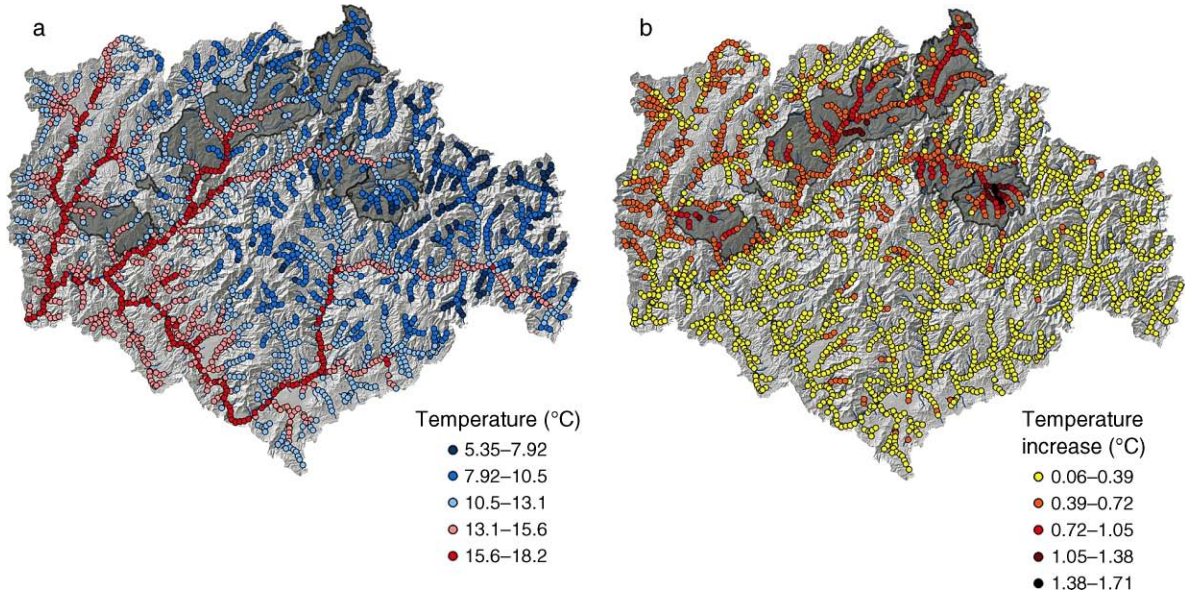
Fig. 5. Thermal maps for the Boise River basin of (a) predicted mean stream temperatures in 2006 and (b) mean temperature changes from 1993 to 2006. Dark gray shaded areas show wildfire perimeters from 1993 to 2006.

TABLE 5. Changes in basin-scale bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*) thermal habitats due to stream temperature trends from 1993 to 2006.

Habitat quality	Year	Habitat patches	Suitable stream length (km)	Patch size (km)		No. patches	
				Mean	Maximum	>10 km	>40 km
Bull trout, mean							
High	1993	158	697	4.41	58.0	13	2
	2006	153	555	3.63	58.0	8	2
	Change	−3%	−20%	−18%	0%	−38%	0%
Suitable	1993	184	1393	7.57	107.4	28	7
	2006	183	1246	6.81	107.4	25	6
	Change	−1%	−11%	−10%	0%	−11%	−14%
Bull trout, MWMT							
High	1993	162	557	3.44	58.0	10	1
	2006	150	433	2.89	55.0	7	1
	Change	−7%	−22%	−16%	−5%	−30%	0%
Suitable	1993	212	1234	5.82	107	22	7
	2006	211	1086	5.15	90.8	17	5
	Change	0%	−12%	−12%	−15%	−23%	−29%
Rainbow trout, mean							
High	1993	185	938	5.07	50.1	23	2
	2006	194	993	5.12	49.5	27	4
	Change	5%	6%	1%	−1%	17%	100%
Suitable	1993	1	2353	2353	2353	1	1
	2006	1	2443	2443	2443	1	1
	Change	0%	4%	4%	4%	0%	0%
Rainbow trout, MWMT							
High	1993	214	1361	6.36	83.5	33	5
	2006	236	1337	5.67	77.2	30	5
	Change	10%	−2%	−11%	−8%	−9%	0%
Suitable	1993	1	2592	2592	2592	1	1
	2006	1	2634	2634	2634	1	1
	Change	0%	2%	2%	2%	0%	0%

Note: MWMT is maximum weekly maximum temperature.

Suitable patches   High-quality patches

Rainbow trout

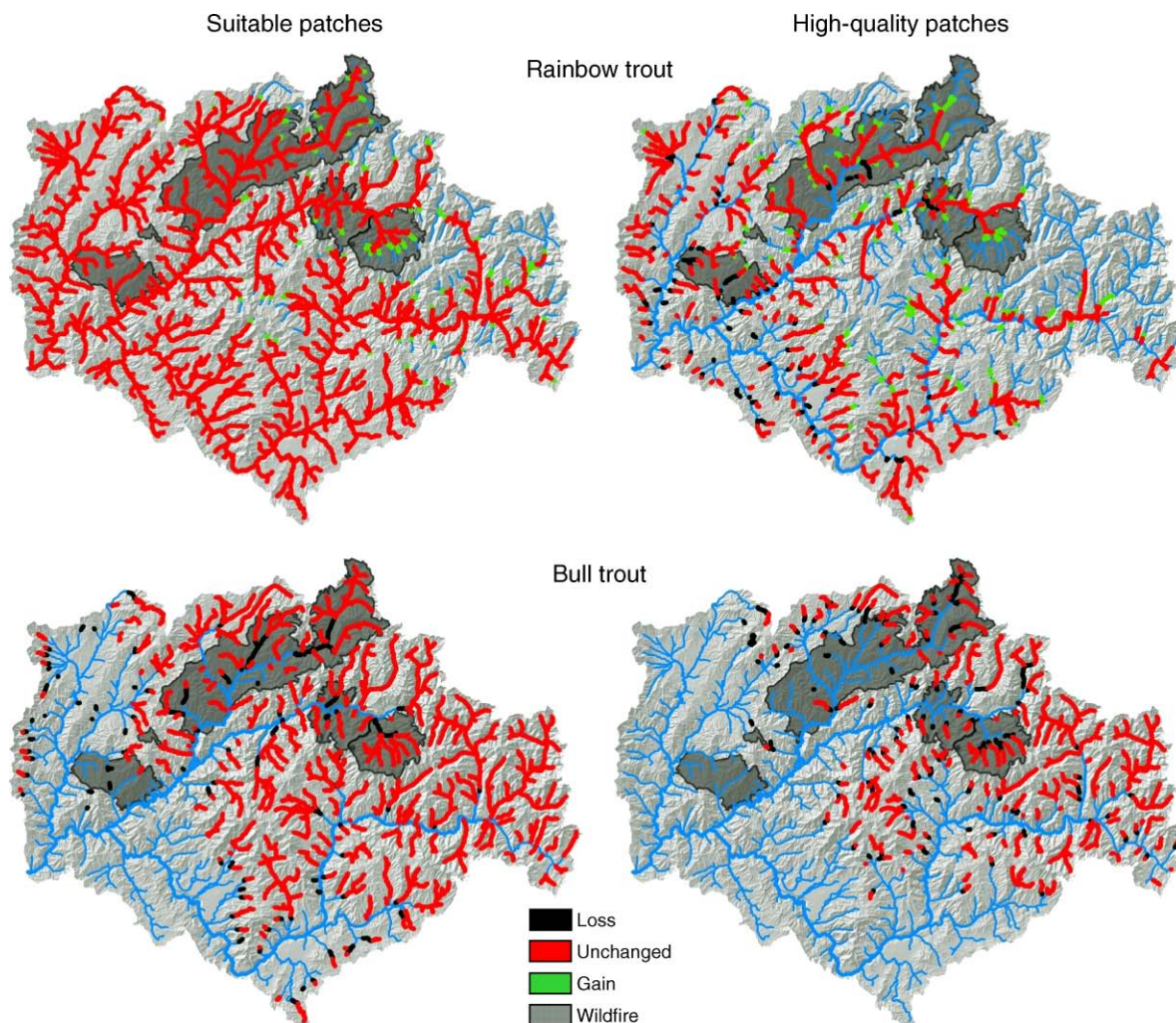Bull trout

Loss
Unchanged
Gain
Wildfire

Fig. 6. Shifts in distribution of thermally suitable stream habitat for rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) natal areas in the Boise River basin from 1993 to 2006 based on observed fires and long-term trends in stream flow and air temperature. Dark gray shaded areas show wildfire perimeters from 1993 to 2006.

items, and increase fish growth rates and densities (Rieman et al. 1997a, Dunham et al. 2007, Koetsier et al. 2007). Upstream habitats that become thermally suitable for rainbow trout may also be in better physical condition than lower elevation streams that tend to be more accessible and compromised by human activities (e.g., Rieman et al. 2000). Although differences in physical characteristics between gained and lost habitats could have important implications for the expression of different life histories (e.g., Brannon et al. 2004), at this point it does not appear that the effects of climate change will dramatically alter the status of rainbow trout in this basin.

Bull trout appear to be more vulnerable. Our results suggest that climate change may be rendering 8–16% of thermally suitable natal stream lengths unsuitably warm each decade. If recent trends continue in the future (when most climate models project accelerated warm-

ing), bull trout may lose half of their habitat in the BRB by mid-century. These losses would be exacerbated by fragmentation of large habitat patches and decreases in connectivity among remaining habitats (Rieman et al. 2007). Because the occurrence of bull trout populations is strongly associated with the size and isolation of habitat patches (Rieman and McIntyre 1995, Dunham and Rieman 1999), ongoing reductions would almost certainly be problematic for persistence of many populations. Moreover, predicted loss rates for the coldest, high-quality habitats were greater than loss rates of suitable habitats. Especially cold streams may be disproportionately important for bull trout persistence within a landscape because they provide thermal environments that are less susceptible to nonnative trout invasions (Rieman et al. 2006, McMahon et al. 2007) and support higher densities of individuals that could

provide emigrants and demographic support to weaker populations.

Most stream temperature increases and habitat shifts within the BRB were related to trends in air temperature and stream flow, but wildfires also had important effects. Our estimates of temperature increases associated with fire were smaller (typically $<1°C$) than the several degree increases that are often reported (e.g., Minshall et al. 1997, Dunham et al. 2007, Leach and Moore 2008), but our study averaged across multiple burn severities and stream types within burn perimeters. Moreover, conclusions from previous studies are difficult to generalize, given their opportunistic nature and tendency to focus on severely burned streams. Despite a smaller estimated effect, however, the wildfires within the BRB effectively doubled or tripled stream warming rates relative to basin averages and caused some of the most dramatic shifts in thermal habitat. If the frequency and extent of wildfires continues to increase (McKenzie et al. 2004, Westerling et al. 2006), greater overlap with shrinking bull trout habitats could foreshadow a difficult future for the conservation of this species in some portions of its range (Rieman et al. 2007).

Within this evolving context, key questions emerge regarding where future fires and other disturbances are likely to occur, their extent, grain of fire behavior and severity, and the processes of postfire population and habitat recovery. In some instances, we have partial answers to these questions or the tools necessary to begin to address them. For example, fire behavior models exist that could be used to simulate wildfire behavior across complex landscapes, but these have yet to be applied in ways that might inform assessments of thermal conditions in streams (Whitlock et al. 2003). We also know that thermal recovery from fires happens, but the process is complex and dependent on prefire vegetation types, burn severity and extent, stream size, and postfire channel disturbances such as debris flow torrents that can retard recovery of riparian areas (Dunham et al. 2003b, Pettit and Naiman 2007). In some streams, thermal effects are minimal and recovery is rapid, but in others, changes may persist for decades after a fire (Minshall et al. 1997, Dunham et al. 2007). Moreover, changing climatic conditions could alter disturbance and recovery trajectories, either by increasing the extent or severity of fires and postfire disturbances or prolonging, possibly even preventing, regrowth of prefire vegetation types (Whitlock et al. 2003, van Mantgem and Stephenson 2007). More details regarding these uncertainties and the changing role of wildfire are needed to refine current understanding and incorporate potential effects into future risk assessments for bull trout or other aquatic species (Bisson et al. 2003, Dunham et al. 2003a).

Whether bull trout are yet responding to habitat shifts, as has been documented for numerous other plant and animal taxa, is unknown (Parmesan and Yohe 2003, Hari et al. 2006, Heino et al. 2009). Although climate-related reductions of natal habitats may have been ongoing for several decades, systematic and spatially representative population monitoring has not been conducted over a similar time frame. Where long-term distributional data do exist for bull trout or other salmonid species, monitoring has typically focused on areas with high fish abundance in the best habitats, which may also be some of the slowest to change (Rieman and McIntyre 1997, Isaak and Thurow 2006). Recognizing this, we have begun to conduct our own distributional assessments, wherein bull trout are resampled along longitudinal profiles that span the lower elevation limit of juvenile fish (Rieman et al. 2006; D. Isaak, *unpublished data*). Preliminary results from 12 streams in central Idaho (seven were in the BRB) suggest that the lower elevation limit of juvenile bull trout did not change consistently across streams between 1997 and 2007, except in three streams affected by fires. Interannual variation may have been too great or the monitoring period too short to detect any population shifts. Because bull trout are a relatively long-lived species (generation time of 5–7 years) with diverse life histories, population responses could be protracted (Morris et al. 2008). Resolving the mechanisms by which climate affects recruitment processes and restricts distributions in streams will ultimately be necessary to accurately predict population responses, but appropriate monitoring strategies are also needed to provide early indications of population shifts and determine rates of change (e.g., Isaak et al. 2009). Monitoring that focuses on the thermally sensitive downstream limits of distributions (e.g., Rieman et al. 2006) could be particularly effective at resolving biological responses in headwater species such as bull trout.

Spatial statistical stream temperature models

Climate change effects on stream temperatures have been assessed in large rivers using mechanistic models (e.g., Gooseff et al. 2005, Flint and Flint 2008) and based on simple statistical relationships between air temperatures and stream temperatures (e.g., Eaton and Scheller 1996, Mohseni et al. 2003). Both approaches provide limited spatial inference, however, because of difficulties associated with extrapolating beyond areas where measurements are obtained. The ability to make valid spatial inference is greatly improved by Ver Hoef and Peterson's new spatial models for streams (Ver Hoef et al. 2006, Ver Hoef and Peterson 2010). These models overcome many of the problems that have limited statistical analyses of stream systems by accommodating spatially complex covariance structures associated with network topology, flow volume, and flow direction (Peterson et al. 2006, Peterson and Ver Hoef 2010, Ver Hoef and Peterson 2010). Incorporating a realistic covariance structure minimizes potential bias in parameter estimates that could arise from spatial autocorrelation (Legendre 1993) and makes the models well-suited for application to "found" databases such as our

PLATE 1. Adult bull trout staging near a spawning area in central Idaho's Salmon River basin (USA). Photo credit: Russ Thurow.

temperature data that are often characterized by clustering and nonrandomness (e.g., Kadmon et al. 2004, High et al. 2009). Moreover, at least from a spatial modeling perspective, spatial autocorrelation is clearly a positive characteristic because it improves the predictive ability of the models (Ver Hoef 2002), as local deviations from the mean response can be modeled using the spatial autocorrelation between nearby sites (Cressie 1993).

Current applications of the stream spatial models have been limited primarily to understanding water chemistry attributes (e.g., Peterson and Urquhart 2006, Peterson et al. 2006, Gardner and McGlynn 2009), but comparable benefits may be expected for biological attributes of stream networks and numerous applications can be envisioned that draw on large georeferenced databases now routinely compiled by natural resource agencies. The integration of spatial models for stream networks with improving ability to characterize important landscape and stream habitat features through GIS promises to significantly advance understanding of lotic ecosystems by reducing much of the imprecision associated with larger-scale inquiries (Fausch et al. 1988, McIntire and Fajardo 2009) and should be particularly useful for understanding relationships at landscape to regional scales.

Air temperature–stream temperature relationships

Air temperature serves a useful role in understanding temporal variability in stream temperature (Mohseni et al. 1998, Caissie 2006) and is commonly used as a surrogate in assessing potential climate change impacts (e.g., Keleher and Rahel 1996, Rieman et al. 2007). Although our analysis suggested air temperatures played a dominant role in stream temperature increases across the BRB, air temperature parameters were considerably less than 1 (MWMT = 0.23; mean = 0.48) and were at the low end of the range reported by Morrill et al. (2005) in a recent review of the subject. Morrill et al. (2005) also note that the smallest air temperature parameters were associated with high-elevation streams, which implies some generality among these systems that may make them less sensitive to future air temperature increases. Multiple factors could contribute to decreased sensitivity, but at the global scale considered by Morrill et al. (2005), strong distinctions would certainly be expected between lowland streams characterized by rainfall hydrology and high-elevation streams dominated by snowmelt runoff and seasonal influxes of cold groundwater. And even within high-elevation streams, variation in sensitivity to air temperatures is apparent seasonally due to variation in snowmelt inputs (Webb and Nobilis 1997, Mohseni et al. 1998) and might also be expected along an elevational gradient from greater snow accumulation and persistence at higher elevations (Luce and Tarboton 2004).

Within the BRB, we speculate that a similar elevational mechanism, perhaps enhanced by greater proportional influences of glacial valleys at high elevations, could have accounted for the small bias in our final temperatures models wherein over- (under-) predictions were made for the coldest (warmest) streams. Because

the spatial models we applied lacked a true temporal component, they could not account for spatially varying sensitivities to air temperature, but instead assumed a spatially uniform effect across the basin. The accuracy of our final stream temperature models attests to the general adequacy of this approach, but an important area of future research would explore the factors responsible for spatial variation in warming rates within and among streams.

Management implications

Our models suggest climate change will have important implications for species such as bull trout, although biologically significant changes may take a decade or more to occur. This time lag may provide a window of opportunity for management actions to conserve or recover some resilience in vulnerable populations. One alternative is to mitigate past habitat disruptions to minimize cumulative stresses and increase resilience against future climate effects. Fortunately, the thermal gains associated with many stream modifications and natural disturbances may be similar to, or larger than, those expected from future climate warming. Riparian vegetation, for example, strongly affects near-stream microclimates (Moore et al. 2005), and minimizing near-stream disturbances associated with grazing, road-building, and timber harvest, or facilitating rapid vegetative recovery after these disturbances, could help buffer many streams from additional warming. Suppression of fires in riparian areas may preclude the most dramatic stream temperature increases and might be warranted where critical habitats or small populations of sensitive fishes occur, but such effects must be weighed against longer-term benefits to stream and forest diversity (Reeves et al. 1995, Rieman et al. 2000). Restoring stream flows or precluding future water abstractions through water right acquisitions are yet other options for buffering streams against warming where flow diversion is an issue.

In addition to thermal mitigation, efforts to increase biological resilience will also be important. Structural barriers associated with road crossings, water diversions, or dams often impede fish movements but can be modified to facilitate fish passage (Fausch et al. 2006). Improved passage promotes connectivity among habitats and may allow populations the flexibility to track habitat distributions that shift with warming or to use refugia when large disturbances occur. If costs of passage improvements are prohibitive, human-assisted migrations may be an option in extreme cases (McLachlan et al. 2007). Within certain contexts, populations of brook trout (or other nonnative salmonids) that constrain downstream distributions of bull trout (or other native species) may be controlled to expand access to local habitats (Moore et al. 1986, Peterson et al. 2008). Promoting diversity, both in terms of life histories (Rieman and Clayton 1997, Isaak et al. 2003) and heterogeneity of stream and forest habitats,

could also minimize risks from large, synchronous disturbances. Although rarely viewed as a viable option, letting populations go in areas where climate impacts will overwhelm restoration potential may also become necessary so that limited resources can be expended more effectively elsewhere. Exercising this option, however, is likely to encounter significant socio-political impediments and will require explicit recognition of management priorities and trade-offs (Bottrill et al. 2008).

Conclusion

Mountain streams in the western United States figure prominently in regional conservation efforts for many species (Thurow et al. 1997, Lee et al. 1998, Kareiva et al. 2000) because they provide relatively pristine habitats in comparison to lower elevation streams where anthropogenic impacts are pervasive. In an era of global warming, however, mountain environments can no longer be viewed as refugia from these impacts. Our work and that of many others (Mote et al. 2005, Westerling et al. 2006, Abatzoglou and Redmond 2007, Hamlet and Lettenmaier 2007, Hamlet et al. 2007, Barnett et al. 2008, Morgan et al. 2008) suggest that rapid climate change within the western United States is effecting profound changes in many environmental drivers that either directly or indirectly affect stream ecosystems. Alteration of stream thermal regimes is likely to be one of the most important environmental changes that aquatic organisms experience, given the strong control that temperature has on distribution, abundance, growth, and population persistence. Some species in certain contexts will benefit from temperature increases, whereas others will experience habitat declines that could significantly reduce the probability of population persistence within individual landscapes or across distributional ranges (Battin et al. 2007, Rieman et al. 2007). But even where negative impacts are anticipated, many populations may persist, especially with assistance from informed, proactive management.

A key challenge will be predicting relative vulnerabilities of populations and habitats so that prioritization can proceed accordingly. Because conservation needs will often exceed available resources, potential management interventions should be viewed in larger contexts to identify those areas where investments are most likely to yield meaningful biological returns (Roni et al. 2002). Broadscale assessments of climatic threats could be used to provide strategic overviews (e.g., Battin et al. 2007, Rieman et al. 2007) and differentiate portions of a species range into future strongholds, lost causes, and areas where management could play a decisive role. In this latter category, more detailed analyses are warranted and could be used to guide conservation planning and project-level implementation at scales relevant to local population persistence. Our approach to statistically downscaling climate change effects on thermal regimes in river networks is a useful step in this regard that helps

reduce many key uncertainties. Although thermal effects will be a first-order determinant for many aquatic species, these considerations need to be supplemented and refined by a better understanding of the mechanisms associated with biological responses, climate effects on other habitat features, and habitat configurations that confer population resilience. As these uncertainties are resolved, those working with stream ecosystems will be increasingly well equipped to conserve biodiversity in a warming world.

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APPENDIX A

Temporal sequence of stream temperature records from the Boise River basin (BRB) used to parameterize temperature models (*Ecological Archives* A020-046-A1).

APPENDIX B

Changes in riparian vegetation determined from Thematic Mapper satellite imagery relative to wildfire perimeters within the BRB between 1989 and 2002 (*Ecological Archives* A020-046-A2).

APPENDIX C

An example of riparian vegetation classifications derived from Thematic Mapper satellite imagery before a wildfire in 1989 and after fire in 2002 (*Ecological Archives* A020-046-A3).

APPENDIX D

Relationships between radiation, watershed area, and vegetation class used to predict radiation values for the stream network in the BRB (*Ecological Archives* A020-046-A4).

APPENDIX E

Stream temperature thresholds used to delineate habitat quality for bull trout and rainbow trout (*Ecological Archives* A020-046-A5).

APPENDIX F

Correlations among variables at 780 sites used in stream temperature models for the BRB (*Ecological Archives* A020-046-A6).

APPENDIX G

Semi-variograms of the residuals from the final maximum weekly maximum temperature (MWMT) and summer mean spatial stream temperature models (*Ecological Archives* A020-046-A7).

APPENDIX H

Percentage of the residual error structures in the final spatial stream temperature models attributable to tail-up, tail-down, Euclidean, and nugget portions of the covariance structure (*Ecological Archives* A020-046-A8).

Hydrogeomorphic effects on bedload scour in bull char (Salvelinus confluentus) spawning habitat, western Washington, USA.

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Introduction

Salmonids have adapted to the natural discharge regimes of fluvial ecosystems (Lytle and Poff 2004). However, embryos of many salmonid species are present in the streambed before and during flood events that transport bedload, e.g., with fall-spawned embryos and winter floods or spring-spawned embryos and early summer floods. Streambed scour (lowering of the streambed elevation) and fill during bedload transport can result in high mortality of incubating salmonids (e.g., Seegrist and Gard 1972; Erman et al. 1988).

The effects of scour on salmonid distribution and abundance at local to regional scales depends on fish size, life history strategy (i.e., iteroparity vs. semelparity), spawn time, amount of spawning and rearing habitat, local hydraulics, geomorphic reach type, sediment supply, discharge regime, and disturbance history. Montgomery et al. (1999) hypothesized that salmonids will not be able to persist in channel reaches with predictable deep scour during the incubation period ("bed scour hypothesis") unless fish locally bury their eggs below typical scour depths or spawn in sites with locally reduced scour. In low-gradient pool--riffle gravel-bed streams, large-bodied salmon avoid streambed scour by burying their eggs below typical scour depths during bankfull discharge (Montgomery et al. 1996). Bedload disturbance depths in low-gradient gravel-bed streams are on average less than two times the 90th percentile surface particle size ($2*[D_{90}]$) (DeVries 2002).

In coarse mountain channels where the supply of spawning gravel is limited and transport capacity is high, smaller-bodied salmonids with shallow to moderate egg burial depths may not be able to bury their eggs deep enough to avoid scour disturbance (i.e., below $2*[D_{90}]$). In addition, bedload transport and scour processes in channels where smaller-bodied salmonids typically spawn may be different than those active in pool--riffle or plane-bed channels where larger salmon spawn (Montgomery et al. 1999). Alternatively, at the local scale, many aquatic species avoid disturbance by selecting habitats that provide refuge from disturbance, preventing species exclusion at higher spatial scales (reach, segment, or catchment; Sedell et al. 1990).

The specific biology and life history of a salmonid can affect their exposure to scouring floods. For example, migratory bull char (Salvelinus confluentus) in western Washington spawn in cold mountain streams during the fall (September to December), peaking in October (Johnson 1991). They are medium-sized (300-800 mm in length), iteroparous, and long-lived (7-12 years) (US Fish and Wildlife Service 1998). Egg burial depths for migratory females average 10-15 cm (DeVries 1997; Shellberg 2002), which is less than larger fall-spawning Pacific salmon (15-25 cm) (DeVries

1997). Egg and alevin gravel residence times are prolonged and temperature-dependent, with hatching after 90-145 days at 2-4 [degrees]C (McPhail and Murray 1979; Shepard et al. 1984) and up to 220 days until gravel emergence (Goetz 1989; Stutsman and Ogg 2002; Shellberg 2002). These biologic factors put bull char eggs and alevins at high mortality risk from scour during late-fall and early-winter peak flood events. However, bull char iteroparity may spread the risk of offspring mortality over multiple years.

Numerous studies have measured the patterns and processes of scour and fill in the spawning habitat of salmonids (e.g., Rennie and Millar 2000; Schuett-Hames et al. 2000; DeVries 2002; and others). However, most of these studies investigated sediment transport and scour patterns in low-gradient, pool--riffle channel types typically used by large-bodied salmon. Sediment transport in steeper mountain streams has been examined in detail (e.g., Bathurst et al. 1983; Gintz et al. 1996), but only a few studies have measured scour and fill in gravel patches used by smaller salmonids in mountain channel types (Kondolf et al. 1991; Barta et al. 1994).

The aim of this study was to investigate the previously undocumented vulnerability of bull char embryos to scour and fill of spawning gravels during fall and winter floods in mountain drainage basins of western Washington State, USA. It was hypothesized that the magnitude of bedload scour at bull char redds is reduced by the presence and selection of stable habitat refugia controlled by local-, reach-, or subcatchment-scale hydrogeomorphic variables. For example, energy dissipation around large woody debris (LWD) structures may reduce the effective shear stress available for bed scour in spawning gravels upstream or downstream of LWD. This habitat refugia component of the bed scour hypothesis (Montgomery et al. 1999) has not been explicitly tested for bull char or most salmonids in general. Therefore, selected hydrogeomorphic variables (hydraulic habitat unit, channel type, discharge magnitude and frequency, sediment transport regime) influencing measured scour and fill depths in bull char spawning locations were analyzed in three contrasting catchments in western Washington.

Materials and methods

Study reaches

Three study catchments were chosen from known spawning populations of migratory bull char in western Washington, USA: the upper Cedar River, North Fork (NF) Skykomish River, and South Fork (SF) Skokomish River. All three catchments are located in high-relief mountainous terrain in the Cascade or Olympic mountains, with moderate to dense conifer forest cover but different geology and forest land use (Table 1). Within each of the three catchments, two adjacent primary spawning reaches were chosen for detailed analysis, providing six reaches in total with contrasting reach-scale (100-1000 m) channel types (Table 1; sensu Montgomery and Buffington 1997).

Table 1. Summary of physical conditions in different study catchments and reaches.

	North Fork Skykomish	
	Lower Goblin Creek	Below Goblin Creek
Channel type	Forced step--pool	Forced pool--riffle
Gradient, %	1.5-3.5	0.7-1.5

Substrate framework	Boulder/cobble	Cobble/boulder
Spawning locations	Gravel pockets, pool tails	Gravel pockets, lateral bars, side channels
Scour monitors		
Selected	7	7
Nonselected	5	11
Catchment area, [km.sup.2]	12.8	88.4
Elevation range, m	549-2134	488-2134
Reach coordinates	47[degrees]55'10.93"N	47[degrees]54'11.02"N
	121[degrees]18'38.03"W	121[degrees]18'59.70"W
Catchment geology	Metamorphic rock, granodiorite, volcaniclastic deposits	Metamorphic rock, granodiorite, volcaniclastic deposits
Land-use history	Mostly wilderness	Wilderness, logging/roads

South Fork Skokomish

	Above Church Creek	Below Church Creek
Channel type	Forced pool--riffle	Forced pool--riffle
Gradient, %	0.8-1.5	0.8-1.0
Substrate framework	Cobble/gravel	Cobble/gravel
Spawning locations	Lateral bars, gravel pockets	Lateral bars, gravel pockets
Scour monitors		
Selected	10	8
Nonselected	8	0
Catchment area, [km.sup.2]	35.6	52.0

Elevation range, m	305–1524	274–1524
Reach coordinates	47[degrees]28'27.16"N	47[degrees]27'1.99"N
	123[degrees]26'56.91"W	123[degrees]25'45.15"W
Catchment geology	Marine sandstone, marine basalt, glacial--fluvial terrace deposits	Marine sandstone, marine basalt, glacial--fluvial terrace deposits
Land-use history	Mostly wilderness	Logging/roads, wilderness
	Upper Cedar	
	Cedar River near Camp 18	Rex River near Boulder Creek
Channel type	Pool--riffle	Pool--riffle
Gradient, %	0.2–0.7	0.2–0.5
Substrate framework	Gravel/cobble	Gravel/cobble
Spawning locations	Gravel riffles, riffle Crests	Gravel riffles, riffle crests
Scour monitors		
Selected	11	12
Nonselected	10	7
Catchment area, [km.sup.2]	105.4	56.7
Elevation range, m	475–1644	475–1341
Reach coordinates	47[degrees]22'12.03"N	47[degrees]22'17.67"N
	121[degrees]37'25.63"W	121[degrees]41'16.76"W
Catchment geology	Volcaniclastic deposits, andesite flows, Quaternary Alluvium	Volcaniclastic deposits, andesite flows, Quaternary alluvium
Land-use history	Logging/roads, water Supply	Logging/roads, water supply

The pool--riffle reaches of the upper Cedar River (including the Rex River) in the western Cascade Mountains are low-gradient channels with gravel beds armoured in patches and well-connected floodplains (Table 1). Obstructions such as LWD are rare, which is at least partially a result of historic riparian timber harvest. The varying yet abundant supply of gravel-sized particles and local gravel armouring lead to the presumption that gravel-sized bedload is at least partially transport-limited as compared with the available stream power (sensu Bravo-Espinosa et al. 2003). Char spawning typically occurs on straight riffles, riffle crests, or occasionally, side channels without other competing fall-spawning species. These reaches are located near the seasonal inundation zone of the large regulated Chester Morse Lake; however, backwater did not affect the stage, discharge, or water surface slope during the measured winter flood events in the study period.

The forced pool--riffle reaches of the NF Skykomish River below Goblin Creek in the western Cascade Mountains are moderate-gradient, cobble-and boulder-bed channels with numerous LWD, boulder, and bedrock obstructions. The associated floodplains are coarse-grained and well connected with abundant side channels created by large LWD jams or overflow channels. The forced step--pool tributary Goblin Creek is a steep-gradient, cobble- and boulder-bed channel, where pools are forced by LWD jams, boulder obstructions, and bedrock. The armoured cobble- and boulder-bed thalwegs and periodic marginal deposits of gravel in these channel types suggest that gravel particles are supply-limited (sensu Bravo-Espinosa et al. 2003) and only persist in local zones of reduced unit stream power. Char spawning typically occurs on lateral bar gravel deposits, pocket gravels above or below obstructions, and in side channels.

The forced pool--riffle reaches of the SF Skokomish River in the southern Olympic Mountains are moderate-gradient, cobble-bed channels with pools forced by LWD or boulders. These reaches are laterally active with side channels and occasional braids, which build coarse-grained floodplains and erode into glacial--fluvial terrace deposits. The supply of gravel-sized particles is from highly episodic mass wasting and terrace erosion. Transient gravel patches overlying an armoured cobble and boulder bed suggest that gravel particles are supply-limited in these reaches with abundant stream power (sensu Bravo-Espinosa et al. 2003). Char spawning typically occurs on lateral bar gravel deposits or pocket gravels above or below obstructions.

Hydrology of study reaches

In the Cedar and Rex rivers, hydrologic data are available from existing US Geological Survey (USGS) stream gages within the study reaches. In the NF Skykomish and SF Skokomish catchments, existing USGS gages were more than 30 km downstream. Therefore, automatic stage recorders were installed along study reaches with adequate local-scale (1-10 m) and reach-scale (~100 m) geomorphic control (Goblin Creek (NF Skykomish) and SF Skokomish River above Church Creek). Stage-discharge rating curves were developed for each gage according to standard techniques (Rantz 1982).

At USGS gages (Cedar and Rex rivers), the frequency or recurrence interval (RI) of annual peak discharge magnitudes was calculated from gage records in Sumioka et al. (1998). At non-USGS gages, the event frequency was estimated from regional regression equations using basin area and basin mean annual precipitation developed by Sumioka et al. (1998). Flood frequency regression data at non-USGS gages had standard error of prediction of [+ or -]50%. Therefore, flood frequency values at downstream USGS gages were used to validate estimates at non-USGS gages upstream.

Bedload scour and fill measurements

Sliding-ball scour monitors were used to measure scour and fill. They consisted of durable

perforated-plastic golf balls, 4 cm in diameter, strung on 3 mm stainless steel cable, attached to an anchor, and inserted into the streambed (Schuett-Hames et al. 1999; DeVries 2000). Scour and fill depths were measured at 4 cm intervals, with an estimated error of [+ or -]2.5 cm, which is slightly larger than that reported by DeVries (2000) due to an uneven heterogeneous bed. Scour and fill depths were measured both incrementally (i.e., from individual floods) and cumulatively (from multiple flood events). The cumulative maximum scour or fill depth for the incubation season is defined as the maximum extent of scour or fill over the period regardless of smaller, intermediate cycles of scour and fill. In minor flood situations where scour was less than the distance to the first scour monitor ball, only net scour or fill could be measured.

Ninety-six scour monitors were installed in the three main catchments (Table 1). Fifty-five monitors were located adjacent to selected bull char redd sites and 41 were located at nonselected sites (see local site selection below). Reference points on all scour monitors were surveyed into local benchmarks to determine their relative elevation and bed elevations after each event. Thirty-four permanent elevational transects were (re)surveyed at scour monitor locations to document net cross-sectional channel change and the stability of scour monitors following distinct flood events. All sites were monitored over two water years (WY) and incubation seasons: WY 2001 and WY 2002. Sites on the Cedar and Rex rivers also were monitored into WY 2003 and WY 2004 to include a wider range of temporal variation in flood magnitude at these sites.

Local site selection

Scour monitors were installed during late summer 2000 and 2001 prior to spawning to avoid disturbing adults or eggs. A grid pattern of scour monitors (Schuett-Hames et al. 1999) was not used because of the unsuitability of much of the coarse substrate for spawning and the low density of bull char spawning activity. Scour monitor and transect installation locations were chosen according to qualitative assessment of potential char spawning sites (based on depth, velocity, substrate, cover, habitat unit) and local advice from fisheries biologists on recent past (1-2 years) spawning locations. Scour data from only one monitor per spawning patch was used in the analysis.

After fall spawning, scour monitor sites were classified as either selected (S) by bull char or nonselected (NS). Scour data were discarded under the rare instance that monitors were disturbed by spawning fish (n = 3). Sites designated as selected were within 2 m of the redd pit within the same homogenous substrate patch, under the assumption that scour processes were similar between the redd and adjacent bed (Rennie and Millar 2000). Nonselected sites were typically not representative of high quality bull char spawning sites based on habitat-preference data (i.e., depth, velocity, substrate size, distance to wetted edge, distance to cover, temperature, vertical hydraulic gradient) collected during spawning conditions and reported in Shellberg (2002). However, nonselected sites were generally suitable for salmonid spawning as many had been locations of redds by other salmonids in other years (e.g., Oncorhynchus kisutch, personal observation by J. Shellberg). Nevertheless, nonselected sites did not represent the full range of habitat conditions throughout a spawning reach (which were not systematically sampled), but were biased toward sites assessed a priori to have a higher probability of spawning.

The site-selection parameters used are distance to wetted edge and proximity to cover (hydraulic obstructions), both normalized by wetted width. These variables were chosen because of their relation to the main hypothesis that scour is reduced by the availability and selection of stable refugia habitat provided by channel margins or in-channel obstructions. Owing to a lack of systematic sampling of reach habitat conditions, distances to cover and wetted edge were normalized to channel dimensions.

All scour monitor sites (selected and nonselected) were classified by hydraulic habitat unit type (Barta et al. 1994). Based on observations at all stages, hydraulic habitat units were classified as either (i) gravel pockets upstream of obstructions, (ii) gravel pockets downstream of obstructions, (iii) lateral bars, (iv) straight bars (riffle crests and riffles), or (v) side channels. Obstructions consisted of single large wood pieces, LWD jams, or large boulders (>1024 mm). Neither scour monitors nor redds were located immediately under or around obstructions where much localized vortex scour typically occurs. All five hydraulic habitats were not always present in each channel type.

Channel hydraulics

At specific scour monitor sites and longitudinally up- and down-stream, Velcro crest gages (DeVries 2000) were established along channel margins to determine maximum stage heights and water surface slopes. Continuous stage data were established for each crest gage from their relationships with nearby continuous stream gages. Water surface slopes were measured for discharge events at a local scale (12 m centered on cross section) and a reach scale (120 m).

Total boundary shear stress, τ_0 (N·m^{-2}), was estimated at each scour monitor site using the depth–slope product:

$$\tau_0 = \rho_w \, g \, d \, S \quad (1)$$

where ρ_w is the fluid density (kg·m^{-3}), g is the acceleration of gravity (m·s^{-2}), d is the local flow depth (m), and S is the local water surface slope (m·m^{-1}). Equation 1 assumes a steady uniform flow, a flow depth equal to the hydraulic radius in a wide, rectangular channel, and a water surface slope equal to the friction slope (Henderson 1966). Local water surface gradient was used as the appropriate gradient to estimate shear stress (Zimmermann and Church 2001).

In mountainous or forested channels, actual or effective bed shear stress can be reduced by momentum and energy losses due to obstructions, bed forms, bank friction, channel bends, and channel width changes (Buffington and Montgomery 1999a). Initial attempts were made to estimate local effective bed shear stress during flood events using vertical velocity profiles (e.g., Wilcock 1996); however, snow and road closures hampered access during all but a few flood events. Furthermore, total shear stress estimates were not partitioned mathematically because of the lack of supporting data in highly complex mountain channels. Thus, analyses of the driving forces of sediment transport were restricted to total shear stress and flood magnitude–frequency.

Total shear stress measurements were nondimensionalized for comparison by using the Shields' equation:

$$\tau^* = \frac{\tau_0}{D_{50}(\rho_s - \rho_w)g} \quad (2)$$

where τ^* is the dimensionless Shields' parameter, τ_0 is the total boundary shear stress (N·m^{-2}), ρ_s and ρ_w are the sediment and fluid densities (kg·m^{-3}), g is the acceleration of gravity (m·s^{-2}), and D_{50} is the median bed-surface grain size (m) (Henderson 1966). Substrate size distributions in selected and nonselected spawning patches were measured during low discharge periods. Pebble counts consisted of at least 100 particles located entirely in local, relatively homogenous substrate patches (Kondolf 1997), excluding within-patch areas disturbed by spawning.

Statistical analysis

Differences in cumulative maximum scour depths between hydraulic habitat units were analyzed using the non-parametric Kruskal--Wallis (KW) one-way analysis of variance because of small sample sizes, unequal variances, and non-normality. The [chi square] distribution was used instead of the Kruskal--Wallis H distribution because of the differing sample sizes (Zar 1999). Differences in scour depth between habitat types were assessed within the selected and nonselected groups but were not compared between groups (selected vs. nonselected) because of the varying representativeness of nonselected sites. The KW test was also used to compare normalized distance to wetted edge distributions with a uniform distribution, representing no selection preference. Linear regression t tests were used to determine whether regression slopes were significantly different from zero. All statistical results were considered to be significant at [alpha] [less than or equal to] 0.05.

Results

Hydrology

Bedload scour and egg mortality within salmonid redds are highly dependent on the probability of peak flood events occurring during the incubation period (October to March). Shellberg (2002) and Gibbins et al. (2008) provide an assessment of discharge regimes in regional bull char catchments and determine the inherent probabilities of flooding during incubation. From their analysis, catchments dominated by rain or rain-on-snow peak flood events such as the SF Skokomish River have a high probability of peak discharges occurring during the incubation period of bull char. Catchments at a slightly higher elevation such as the upper Cedar and Skykomish rivers have a moderate probability of peak discharges occurring during this period because of the influence of seasonal snow packs. The timing of different flood events and their different flood-producing mechanisms (rain, rain-on-snow, snowmelt) are evident in the study area hydrographs (Fig. 1).

During the study period, WY 2001 was one of the driest winters on record, with peak discharges at or less than the 1-year recurrence interval (RI) in all study catchments. In contrast, WY 2002 had normal precipitation and discharge, and WYs 2003 and 2004 experienced above-average precipitation and peak discharge (Fig. 1).

Local bedload scour at redd sites

During the WY 2001 drought (Fig. 1), minimal bedload transport at all selected (S) and nonselected (NS) scour monitor sites resulted in shallow scour depths (<5 cm), lack of channel change, and high survival to emergence of char (e.g., Stutsman and Ogg 2002). After additional spawning site selection during the WY 2002 char spawning season, sites selected by bull char during both WY 2001 and WY 2002 were combined as one data set for analysis because of the low number of selected sites for any given year and the unchanged bed morphology from the previous year.

NF Skykomish River

Three flood events (14 November 2001, 7 January 2002, and 22 February 2002) occurred during WY 2002 (Figs. 1c--d), which had RIs ranging from approximately 1 to 3 years. The cumulative maximum scour depth for the entire WY 2002 winter egg incubation period (October to March) was significantly different between hydraulic habitat units selected (KW p [less than or equal to] 0.03) and not selected (KW p [less than or equal to] 0.02) by bull char (Fig. 2a). Among selected sites, lateral bars experienced the greatest scour depths (>10-15 cm) at or beyond cited egg burial depths (DeVries 1997). Sites downstream of obstructions such as LWD and boulders had moderate

amounts of scour (generally <10 cm), whereas selected side-channel spawning sites were stable with a tendency toward fill. These results support the hypothesis that specific hydraulic habitat units such as side channels and units near obstructions can provide incubation environments with reduced scour.

[FIGURE 2 OMITTED]

SF Skokomish River

Cumulative maximum scour depths during WY 2002 were dominated by events on 16 December 2001 and 7 January 2002, which were both between the 2- and 4-year RI. Scour depths at many selected and nonselected sites were at or well beyond the 10-15 cm cited egg burial depths (Fig. 2b), indicating that substantial egg loss could result at these discharge magnitudes, as supported by Stutsman and Ogg (2002). Selected sites upstream of LWD obstructions experienced significantly less scour (KW p [less than or equal to] 0.02), as these sites continued to be deposition zones for locally eroded gravel. Sites downstream of obstructions were initially stable in December 2002, but eventually scoured during the observed mobility of modest diameter LWD. Although these results partially support the hypothesis that obstructions can provide incubation environments with reduced scour, they also demonstrate that site-specific discharge thresholds exist at which in-channel obstructions can become mobilized (especially modest-sized LWD), ending their role as energy and scour reducers.

Upper Cedar River

Scour and channel change were monitored for two additional years in the Cedar and Rex rivers (WYs 2003 and 2004), providing additional data for the relationship between scour depth and flood recurrence interval. Cumulative maximum scour depths during both WY 2001 and WY 2002 were shallower than cited egg burial depths except for a few extremes (Fig. 3). Cumulative maximum scour during WY 2002 was dominated by one flood event on 14 April 2002 (Cedar River, 1.8-year RI; Rex River, 1.3-year RI), when slight fill was just as common as scour and a majority of the bed was not mobilized. During WYs 2001 and 2002, abundant production of bull char was determined from qualitative observations of juveniles (J.G. Shellberg and local biologists' personal observations). Each year from 2001 to 2004 generally had progressively higher peak discharge magnitudes (Figs. 1a and 1b) resulting in progressively deeper scour depths at or beyond the 10-15 cm egg burial range during WY 2004 (Fig. 3). However, this deep scour (>15 cm; Fig. 3) was only common during 2004, which had the highest flood durations above the 1.5-year RI during the study (see below). Data from 2001-2003 support the bed scour hypothesis that vertical refugia may exist below 2*[D.sub.90] during common flood events in partially transport-limited, pool--riffle channel types with abundant gravel and local gravel armour layers.

[FIGURE 3 OMITTED]

Shear stress at scour monitor sites

In the NF Skykomish catchment, scour depth data at side-channel, downstream, and lateral bar habitat units were correlated as one group against estimates of total bed shear stress from the depth--slope product during the largest flood event in WY 2002 (7 January 2002) (Fig. 4). Although the above habitat units were characterized by systematically different local shear stresses, the units were situated on an increasing gradient of exposure to shear stress, as supported by local velocity profiles in Shellberg (2002). Therefore, they were analyzed together to develop a common relationship between shear stress and scour depth (Fig. 4). Overall, the surface of lateral bars had

the highest total shear stress estimates and experienced the deepest scour, but deep scour beyond 2.5*[D.sub.90] was uncommon. The best-fit logarithmic trend suggests an asymptotic trend with a limit on potential scour depth; however, this needs to be confirmed by sampling scour over a larger range of discharges and shear stresses than observed in this study. According to these total shear stress estimates, the initiation of scour (motion) began at a dimensionless shear stress value of ~0.05, similar to values reported elsewhere (Buffington and Montgomery 1997).

[FIGURE 4 OMITTED]

In contrast with the NF Skokomish, the relationship between shear stress and scour depth in the SF Skykomish varied between habitat types because of large differences in local depth and slope and presumably differences in energy dissipation (Fig. 5); therefore, units were analyzed separately. In all habitat units, scour depth (scaled to [D.sub.90]) increased significantly with dimensionless shear stress, but the rate of increase varied among different hydraulic habitat units. Lateral bar sites with relatively little structural energy dissipation had total dimensionless shear stresses closest to the presumed local effective stress (i.e., initiation of scour at ~0.05) (Fig. 5). Scour at sites upstream and downstream of obstructions began at higher dimensionless boundary shear stresses of ~0.1 and 0.2, respectively, indicating that actual effective shear stresses were greatly reduced by energy dissipation around these structures and (or) that the local depth--slope product greatly overestimated total shear stress in these locales.

[FIGURE 5 OMITTED]

In the upper Cedar River reaches, cumulative maximum scour depth increased ([r.sup.2] = 0.21, p < 0.0001) with increasing total dimensionless shear stress estimated for the largest flood event of each year (Fig. 6). The initiation of scour (motion) also began at dimensionless shear stress values near ~0.05, which was likely due to the dearth of obstructions influencing energy loss in these pool--riffle channel types. However, the variability in the relationship between scour and shear stress was considerable due to the tendency for both scour and fill in these channel types, plus the lack of more precise data on local sediment supply imbalances and local effective shear stress.

[FIGURE 6 OMITTED]

Despite the lack of local effective shear stress measurements, total shear stress measurements applied locally in these different channel types and hydraulic habitat units demonstrate that both shear stress and scour are reduced in spawning gravels near in-channel obstructions and in side channels. These habitats provide scour refugia for incubating bull char embryos according to the main hypothesis. Data from the pool--riffle channels of the upper Cedar River highlight that other factors beyond obstructions can influence shear stress and resultant scour and fill, e.g., alternating bedforms (pools and riffles) and storage of abundant gravel.

Reach-scale bed mobility

In the NF Skykomish catchment, data from elevational transects before and after floods confirmed that the framework structure of the channel bed (i.e., large interlocked cobbles and boulders) was stable during common flood events (<3-year RI). Annual net change in cross-sectional area ranged from -1.3% to 4.4% (median of 1.1%, n = 6) (positive values indicate degradation). However, local exposed and unprotected gravels in lateral bars were mobile and experienced scour (Fig. 2a), indicating a different threshold of mobility for habitat units with contrasting particle sizes (e.g., Gintz et al. 1996; Zimmermann and Church 2001).

The transects of the Cedar and Rex rivers also were generally stable in their morphology during four years of monitoring, despite patchy local scour and fill in spawning riffles (Fig. 3). During WY 2002, net annual change in channel cross-sectional area ranged from -2.3% to 8.6% (median of 0.5%, n = 11). From WY 2003 to WY 2006, cumulative net change in channel cross-sectional area increased (range, -9.6% to 14.8%), but the median value remained low (-0.3%, n = 11). Local gravel armor layers were only breached during events greater than the 2-year RI. It remains unknown whether larger discharges (i.e., >4.0-year RI) would produce even greater channel change and scour depths, or whether this relationship would break down because of the difficulty of shearing abundant gravel to great depths in pool--riffle channel types (DeVries 2000, 2008).

In contrast to other catchments, the SF Skokomish transects showed considerable reach-scale bed mobility. Above Church Creek, temporary sediment transport imbalances were associated with eroding terrace deposits at cut banks. Initial aggraded material (sand, gravel, cobble, LWD) was stable and attractive to spawning bull char in an otherwise coarse cobble-bedded reach. Spawning gravels were partially unstable during the first few floods of the year (1- to 2-year RI), when the change in cross-sectional area ranged from -2.7% to 7.4% (median, 1.9%; n = 5). These gravels were later exported during larger events (3.8-year RI), resulting in scour (Fig. 2b) and net increases in cross-sectional area (range, -16.6% to 19.3%; median, 6.0%; n = 5). Newly recruited sediment from terrace deposits re-initiated the cycle of bed aggradation and degradation. Below Church Creek, additional coarse and fine sediment was delivered from both upstream terrace cut bank erosion and anthropogenically enhanced erosion of landslide material (e.g., Church Creek). This reach adjusted more frequently to its imposed sediment supply, resulting in initial scour at or beyond the cited egg burial depths (Fig. 2b), which was later followed by massive aggradation and decreases in net cross-sectional area (range, -15.0% to -69.6%; median, -58.0%; n = 5).

These channel change data suggest that hydrogeomorphic conditions beyond local in-channel obstructions or egg burial depth can influence embryo vulnerability to scour and fill, specifically the stochastic supply, storage, and transport of sand and gravel bed material. Thus, local refugia at the reach scale may be inadequate for scour protection in isolation, and channel segment or subcatchment scale refugia may play an important role.

Redd site selection and scour refugia

Redd distances to wetted edge, normalized by wetted width, were typically less than 0.30 for both the NF Skykomish and upper Cedar sites, suggesting that fish generally avoided the center 40% of these channels. However, selected sites did not have distributions significantly different from a uniform distribution (NF Skykomish, KW p > 0.5; upper Cedar, KW p < 0.12), indicating that any width selection preference was slight. In contrast, the SF Skokomish had normalized distances to wetted edge values less than 0.10. Selected sites differed significantly (KW p < 0.0001) from a uniform distribution, suggesting a strong selection preference for channel margins. However, avoidance of deep thalwegs in the SF Skokomish also was partially influenced by limited gravel availability in these areas.

Redd distance to cover was largest in the pool--riffle reaches of the upper Cedar River (median, 12.2 m; range, 1.2-21.3 m), where the forced pool--riffle channels of the NF Skykomish (median, 2.9 m; range, 1.8-5.5 m) and SF Skokomish (median, 5.5 m, range 2.3-8.8 m) had lower values. In comparison to available habitat, values normalized to wetted width were lowest in the SF Skokomish (median, 0.21; range, 0.16-0.49), intermediate in the NF Skykomish (median, 0.55; range, 0.07-0.70), and highest in the upper Cedar River (median, 0.62; range, 0.10-1.09).

Site selection in proximity to potential scour refugia (channel margins or obstructions) was most

pronounced in the SF Skokomish River, less pronounced in the NF Skykomish, and relatively absent in the pool--riffle reaches of the upper Cedar River. It is interesting to note that the scour sites and reaches in the SF Skokomish in the Olympic Mountains had the deepest scour depths, the greatest degree of reach-scale bed mobility, and the most inhospitable discharge regime (Figs. 1e, 1f; Gibbins et al. 2008), supporting the hypothesis that bull char were actively selecting spawning sites to avoid redd scour.

Flood discharge and scour

The three catchments and channel types had median scour depths at or beyond the cited egg burial depths (10-15 cm) during 2- to 4-year RI events, suggesting that bull char redds are indeed vulnerable to scour during common flood events. When grouping scour data for all study sites, positive trends existed for increasing scour or median scour with increasing RI, respectively ($[r.sup.2] = 0.20$, $p < 0.0001$; $[r.sup.2] = 0.70$, $p < 0.0001$) (Fig. 7a). However, the distribution of local scour depths differed at the hydraulic habitat unit scale and between channel types (Figs. 2-6), presumably due to variations in local shear stress and sediment supply. The exception of increasing median scour with increasing RI was the Cedar River, where the largest flow magnitude during WY 2003 (3.8-year RI) was higher than during WY 2004 (3.1-year RI) (Fig. 1a), whereas the opposite was true for scour depths. However, the total time duration that discharge exceeded the 1.5-year RI was greater in 2004 than in 2003. Positive trends also existed between scour or median scour and flood duration ($[r.sup.2] = 0.21$, $p < 0.0001$, and $[r.sup.2] = 0.86$, $p < 0.0001$, respectively) (Fig. 7b). Although total flood duration greater than the 1.5-year RI is intuitively a more meaningful hydrologic metric to relate to net scour over an entire water year (rather than one peak flood RI value), the correlation with scour only improved slightly, partially due to the positive correlation between annual peak RI and total flood duration ($[r.sup.2] = 0.73$).

[FIGURE 7 OMITTED]

Discussion

The results show that fall-spawned bull char redds are indeed vulnerable to bedload disturbance and scour in rain or rain-on-snow dominated catchments in western Washington during relatively common flood events (2- to 4-year RI). However, redd scour is dependent on many site-specific hydrogeomorphic factors that vary between different catchments, channel types, habitat units, and discharge and sediment regimes. In support of the main hypothesis, bull char did select sites that provided reduced bedload scour such as local sites near LWD and boulders or in side channels created by complex fluvial processes at the reach scale. In addition, egg burial depth below gravel armour layers and typical scour depths appeared to be a viable refuge strategy during common flood events in pool--riffle channel types with few in-channel obstructions. Certain catchment discharge regimes (i.e., winter rain or rain-on-snow dominated), sediment supply regimes (i.e., enhanced mass wasting), reach-scale channel types (i.e., supply-limited reaches), and habitat units (i.e., unprotected gravel patches) appear to be high-risk areas for bull char spawning.

Influence of reach type and local habitat type

Reach-scale channel type and morphology strongly influenced the type, availability, and stability of local spawning gravel, as suggested by Montgomery et al. (1999) and Buffington et al. (2004). Gravel deposits were more transient in supply-limited reaches (forced pool--riffle and forced step--pool in this study) compared with partially transport-limited reaches (pool-riffle). Forced pool--riffle reaches influenced by locally high but transient gravel supply and reduced wood loads from altered riparian zones had more mobile channel beds than reaches with modest sediment supplies and

abundant large wood. Gravel deposits associated with energy dissipating structures (LWD or boulders) experienced reduced scour magnitudes, as suggested by Kondolf et al. (1991) and Barta et al. (1994). In pool--riffle reaches, abundant gravel and local gravel armor layers partially mitigated against deep scour (>15 cm) beyond egg burial depth (e.g., DeVries 2000, 2002, 2008), implying that other mechanisms besides in-channel obstructions also can provide refugia from egg scour. Quantitative data in the NF Skykomish and qualitative data in the upper Cedar and SF Skokomish catchments indicate that side channels were the most stable spawning areas utilized by bull char due to dampened stream power across complex floodplain habitat.

Site selection

Bull char spawning site selection indicated a slight to strong preference toward channel margins. Elevational transect and scour data demonstrated that gravel patches along channel center lines and thalwegs were less stable than channel margin areas, especially in compound cross sections, similar to the findings of other studies (Lapointe et al. 2000; Ames and Beecher 2001; Haschenburger 2006). Ames and Beecher (2001) have labeled the relatively scour-free channel margin areas "flood protection zones" (FPZ) because of the high relative survival of salmonid eggs and alevins in these areas. However, in higher gradient channel types, it remains unclear whether spawning site selection is a result of increased spawning gravel availability along channel margins in otherwise coarse channels or selective pressures to avoid sediment transport (scour) along the channel center line during predictable floods (i.e., SF Skokomish). Regardless, there are significant mortality trade-offs between spawning high in a cross section near the channel edge to avoid bedload scour and spawning low in a cross section near the thalweg to avoid redd dewatering or sedimentation (Den Boer 1968; Ames and Beecher 2001; Gibbins et al. 2008).

Successful spawning in pool--riffle reaches with few in-channel obstructions indicates that selection of hydraulic cover is not essential in channel types with generally low scour depths. However, site selection near local cover that provides hydraulic shelter (LWD, boulders) or in reach-scale side channels may enhance the protection of bull char off-spring from deep scour, especially in channel types with higher stream power. Where suitable hydraulic complexity exists at the reach scale, it is hypothesized that the wide site selection proclivities of bull char should result in at least some redds being constructed in areas protected from scour during large floods (i.e., risk-spreading at the subpopulation level). Females occasionally construct multiple redds within a reach (J.G. Shellberg, personal observation), which may also be a site-selection risk-spreading technique at the individual level.

Frequency of disturbance

Sediment transport and scour depths generally increased with discharge magnitude and shear stress, similar to other studies (Emmett and Leopold 1965; Carling 1987; Haschen-burger 2006), with flood discharge RI and duration accounting for up to 20% of variation in scour depths. In catchments in this study, scour to cited egg burial depths did not typically commence until flood events exceeded the 2-year RI. The frequency of disturbance needed to entrain the entire bedload of these reaches and (re)create complex habitat across the channel and floodplain was greater than the 4-year RI, similar to studies on other regional rivers (e.g., Ham and Church 2000; 5-year RI). Floods larger than these observed magnitudes are needed to deposit well-sorted gravel patches below newly formed LWD jams and other obstructions to provide stable habitat during smaller floods. Even larger floods are needed to reset floodplain habitat mosaics and create side channels important for spawning refugia during common floods (e.g., Wondzell and Swanson 1999; Whited et al. 2007). Adapting the intermediate disturbance hypothesis to habitat heterogeneity rather than species diversity (Richards et al. 2002), channel-changing flood events occurring at an intermediate

frequency are important in creating and maintaining complex habitat (e.g., gravel pockets near obstructions and side channels) for aquatic organisms such as bull char.

Shear stress

In addition to flood magnitude and duration, estimates of total boundary shear stress generally improved predictions of scour depth, explaining up to 60% of the variability in scour at some sites. However, other factors such as local effective (grain) shear stress and local sediment supply to specific spawning patches likely explain much of the remaining variability. Future detailed measurements of local hydraulic and velocity conditions (e.g., Wilcock 1996; Crowder and Diplas 2002) should improve local effective shear stress and scour predictions in mountain channel types.

Changes in hydrology and sediment supply

Bull char typically spawn in cold mountain valleys where catchment water, sediment, and LWD production are sensitive to proximal land surface and land use conditions (Church 2002). Building road networks and timber harvesting on potentially unstable slopes can increase the magnitude and frequency of sediment production (e.g., Beschta 1978) and bed mobility in response to altered sediment regimes (e.g., Tripp and Poulin 1986; Madej and Ozaki 1996; Lisle et al. 2000). Changing land cover can also alter water yield (e.g., Harr et al. 1975; Bosch and Hewlett 1982; Harr 1986) and increase the magnitude of common peak flood events (i.e., <1- to 2-year RI up to the 10-year RI) in small- and medium-sized catchments (e.g., Jones and Grant 1996, 2001; Lewis et al. 2001). During this study, scour to cited egg burial depths occurred during these sensitive common peak flood events, as found in other studies (Montgomery et al. 1996; Haschenburger 2006). Changes in event magnitude and frequency could increase the frequency of disturbance of scour in char spawning areas (Tonina et al. 2008), especially if coupled with increased production of transient bed sediment and loss of instream LWD structure.

In this study, the catchments of the NF Skykomish and SF Skokomish above Church Creek remain relatively undisturbed from human activities and produce moderate to low (respectively) numbers of bull char. In contrast, the SF Skokomish River below Church Creek has been affected by the delivery of large amounts of coarse sediment (sand and gravel) from road building and timber harvesting on steep, erodible slopes, resulting in increased bed mobility. Although the upper Cedar River catchment also has been densely roaded and logged, the low-gradient pool--riffle reaches are partially decoupled (sensu Church 2002) from upstream water and sediment supply disturbances. Low stream power, gravel armor layers, and abundant gravel appear to mitigate scour depths in these pool--riffle reaches (e.g., DeVries 2000, 2002, 2008), which support high numbers of bull char. Fine sediment (clay, silt, fine sand) throughput and deposition may be a greater mortality factor in these channel types (DeVries 2008).

From these observations, we hypothesize that anthropogenically increased production of transient bed sediment to supply-limited reaches, especially sand and poorly sorted gravel, increases the frequency of spawning gravel mobility and scour to egg burial depths during relatively common flood events (i.e., 1- to 4-year RI). Bed texture and mobility are sensitive to sediment supply (Buffington and Montgomery 1999b; Lisle et al. 2000). Though large sustained influxes of gravel could force changes in channel type, anthropogenically increased bed material supplies more commonly produce episodic fluxes of poorly sorted sediment that is highly transient. In contrast, the well-sorted spawning gravels that salmonids have adapted to in mountain channels are created as gravel lag deposits in preferential deposition zones that are flushed of finer, more mobile sediment over geomorphic time scales. Thus the caliber and quantity of contemporary sediment supply and bed mobility may be good indicators of spawning habitat integrity. Other studies have noted a negative

relationship between land use intensity (i.e., riparian harvest and roads disturbance) and char population abundance (Baxter et al. 1999).

Loss of roughness

Reduced LWD hydraulic roughness has been predicted to result in reach-scale bed-surface coarsening and a reduction in both the availability and retention of quality spawning substrate (Buffington and Montgomery 1999a; Buffington et al. 2004). Abundant LWD can provide spatial spawning habitat heterogeneity that salmonids actively select for and improve the redd carrying capacity of a reach (Merz 2001), in addition to reducing velocity and shear stress (this study). Bed stability has been shown to decrease following wood removal (Bilby 1984; Smith et al. 1993) and where LWD is undersized and mobile (McHenry et al. 1998; Schuett-Hames et al. 2000; Fox et al. 2002). A loss in the quality, quantity, and diversity of LWD roughness due to riparian logging, instream wood removal, and (or) increased hydrologic flushing may reduce the availability or quality of bull char spawning habitat (Hauer et al. 1999), especially in sediment supply limited reaches with high stream power.

Implications

This study emphasizes the importance of habitat heterogeneity and refugia availability in sustaining salmonid populations at multiple spatial scales: from catchment-scale (10-1000 km) discharge regime heterogeneity and flood disturbance probability, to reach-scale (100-1000 m) channel type complexity, to local-scale (1-10 m) site selection and structural energy dissipation. The distribution and abundance of bull char in western Washington could have been influenced by a loss of complex fluvial spawning habitat (e.g., LWD roughness), especially in streams with limited supplies of quality gravel and harsh discharge regimes during incubation (rain or rain-on-snow dominated). Processes that form complex habitat in association with LWD (Beechie et al. 2000) may partially mitigate against unfavorable discharge regimes, water and sediment yield alterations due to land-use, or future climate change (e.g., Battin et al. 2007).

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Aquatic and Other Environmental Impacts of Roads:
The Case for Road Density as Indicator of Human Disturbance and Road-
Density Reduction as Restoration Target;
A Concise Review
Pacific Rivers Council Science Publication 09-001

by

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Abstract

Roads have well-documented, significant and widespread ecological impacts
across multiple scales, often far beyond the area of the road "footprint". Such
impacts often create large and extensive departures from the natural conditions
to which organisms are adapted, which increase with the extent and/or density of
the road network. Road density is a useful metric or indicator of human impact at
all scales broader than a single local site because it integrates impacts of human
disturbance from activities that are associated with roads and their use (e.g.,
timber harvest, mining, human wildfire ignitions, invasive species introduction
and spread, etc.) with direct road impacts. Multiple, convergent lines of empirical
evidence summarized herein support two robust conclusions: 1) no truly "safe"
threshold road density exists, but rather negative impacts begin to accrue and be
expressed with incursion of the very first road segment; and 2) highly significant
impacts (e.g., threat of extirpation of sensitive species) are already apparent at
road densities on the order of 0.6 km per square km (1 mile per square mile) or
less. Therefore, restoration strategies prioritized to reduce road densities in
areas of high aquatic resource value from low-to-moderately-low levels to zero-
to-low densities (e.g., <1 mile per square mile, lower if attainable) are likely to be
most efficient and effective in terms of both economic cost and ecological benefit.
By strong inference from these empirical studies of systems and species
sensitive to humans' environmental impact, with limited exceptions, investments
that only reduce high road density to moderate road density are unlikely to
produce any but small incremental improvements in abundance, and will not
result in robust populations of sensitive species.

Aquatic and other environmental impacts of roads

Roads have well-documented, significant and widespread ecological impacts
across multiple scales, often far beyond the area of the road "footprint", with
negative effects on biological integrity in both terrestrial and aquatic ecosystems
(Forman & Alexander 1998; Gucinski et al. 2001; Trombulak & Frissell 2000).

These include direct mortality from road construction and vehicle collisions, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotic species and increased human use of areas (Forman 2004; Forman & Alexander 1998; Gucinski et al. 2001; Trombulak & Frissell 2000). Road construction kills stationary and slow-moving organisms, injures organisms adjacent to a road and alters physical conditions beneath a road (Trombulak & Frissell 2000), often including direct conversion of habitat to non-habitat within the road and roadside corridor "footprint" (Forman 2004). Behavior modification depends on species and road size/type, but ranges from road corridor use to avoidance to complete blockage of movement, which fragments or isolates populations, often with negative demographic and genetic effects, and with potential consequences up to and including local population or species extinction and biodiversity loss (Forman 2004; Gucinski et al. 2001; Trombulak & Frissell 2000). Additional behavior modification includes changes in home range, reproductive success, escape response and physiological state (Forman & Alexander 1998; Trombulak & Frissell 2000).

Roads change soil density, temperature, water content, light levels, dust, surface waters, patterns of runoff, erosion and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments (Forman 2004; Gucinski et al. 2001; Trombulak & Frissell 2000). When delivered to streams, these road-derived contaminants reduce water quality (Gucinski et al. 2001). Increased road-derived fine sediments in stream gravel have been linked to decreased fry emergence, decreased juvenile densities, loss of winter carrying capacity, increased predation of fishes, and reduced benthic organism populations and algal production (Gucinski et al. 2001). Roads greatly increase the frequency of landslides, debris flow, and other mass movement (Gucinski et al. 2001). Roads promote the dispersal of exotic species and pathogens by altering habitats, stressing native species, and providing corridors and vehicle transport for seed/organism dispersal (Forman 2004; Gucinski et al. 2001; Trombulak & Frissell 2000). Roads also promote increased hunting, fishing, poaching, passive harassment of animals, use conflicts, lost solitude, lost soil productivity, fires, and landscape modifications (Forman 2004; Gucinski et al. 2001; Trombulak & Frissell 2000). Presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems and habitat (Gucinski et al. 2001; Trombulak & Frissell 2000), including severing connections between streams and adjacent floodplain networks, converting subsurface to surface flow by intercepting groundwater flowpaths and diverting flow to streams, thereby increasing run-off, "flashiness" and erosion (Forman 2004; Gucinski et al. 2001).

In particular, roads have been consistently singled out as a primary cause of the reduced range and abundance of many aquatic species, not only in the West but also across the continent (CWWR, 1996; USFS and USBLM, 1997a; Trombulak and Frissell, 2000; Kessler et al., 2001; Angermeier et

al., 2004). Czech et al. (2000) estimated that roads in the U.S. contribute to the endangerment of some 94 aquatic species. [Rhodes 2007, p. 7]

Road density as indicator of human disturbance to natural systems

Species and biological communities evolve through co-adapting to each other and the physical environment of their native ecosystems. The broad suite of significant road impacts just described often creates large and extensive departures from the natural processes, interactions and conditions to which organisms are adapted, which increase with the extent and/or density of the road network. Road density is also a useful metric or indicator of human impact at all scales broader than a single site because it integrates impacts of human disturbance from activities that are associated with roads and their use (e.g., timber harvest, mining, human wildfire ignitions, invasive species introduction and spread, hunting, fishing, poaching, etc.) along with direct road impacts (Lee et al. 1997; Quigley et al. 2001; Trombulak & Frissell 2000). Thus, an expectation that environmental degradation and associated biological impacts would increase with road density and, conversely, that remaining areas with very few or no roads would be strongholds of imperiled species and native biodiversity (in addition to providing other important ecosystem services such as clean water sources, carbon sequestration, recreation, and solitude) is both logical and obvious.

Objections have sometimes been raised to use of road density as an indicator of disturbance (or reductions in road density as a target for restoration) on grounds that all roads are not equal in ecological impact. However, while the latter is certainly true, validity and utility of road density as a robust indicator for watershed condition and aquatic impact – because of its integration of non-direct road-specific impacts as noted above – has been repeatedly demonstrated and is strongly confirmed by its extensive and repeated recommendation in the Forest Service's guidance for Roads Analysis (USDA Forest Service 1999).

Expectation that road density would be associated with environmental degradation or species declines is further confirmed by empirical evidence finding significant correlations between population/community strength of Threatened, Endangered, Sensitive or other native species or other measures of ecological integrity and roadless proportion or road density. Together, this evidence strongly indicates that significant negative impacts can be detectable beginning with even the first one-tenth-mile of road per square mile of watershed (Lee et al. 1997). Multiple lines of evidence further indicate that substantial water quality declines, watershed degradation, and aquatic species impact must be expected at road densities higher than about 1 mile per square mile (0.6 km per square km) or less. This in turn suggests that – with limited, generally site-specific exceptions – because adverse impacts become evident even at quite low road densities, the greatest restoration efficiency with limited resources will result

from targeting road reduction to high-value watersheds where low-to-moderately-low road densities can be brought below a mile per square mile or less, rather than where moderate-to-high road density would be reduced, but still remain moderate-to-high (exceptions might include a particular high-risk or high-impact road segment directly impacting a specific, high-value population or highly productive habitat of an at-risk species). These lines of evidence include:

- At the landscape scale, increasing road densities and their attendant effects are correlated with declines in the status of some non-anadromous salmonid species (Gucinski et al. 2001).
- For example, Frissell and Carnefix (2007) found a significant relationship between bull trout spawner abundance and proportion of subwatershed area within designated Wilderness or Inventoried Roadless Areas (IRAs) for 19 subwatersheds in the Rock Creek drainage, Granite and Missoula Counties, Montana, and disproportionately high occurrence of native salmonids, including genetically pure populations, associated with IRAs statewide.
- Ripley et al. (2005) surveyed 172 stream reaches located throughout the majority of the lower two-thirds (where industrial activities, mainly timber harvest and roads, are most predominant) of the Kakwa River basin in central western Alberta, Canada, and modeled relationships of bull trout presence and abundance with environmental factors. Bull trout were observed only at road densities (in the subbasin draining to the sampling reach) ranging from 0 to 0.6 km per square km (1 mile 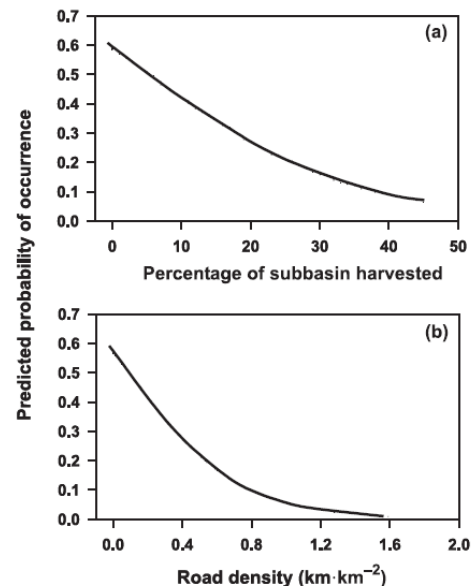per square mile). Road density was generally related significantly and negatively to both bull trout occurrence and abundance in logistic and zero-inflated Poisson (ZIP) regression models. Notably, consistent, steepest decline in the modeled probability of bull trout occurrence fell between 0 and 0.4 km per square km (≈ 0.6 miles per square mile; see their Fig. 2 at right). This is consistent with other

Fig. 2. Logistic regression models of the predicted probability of bull trout (*Salvelinus confluentus*) occurrence and (*a*) percentage of the subbasin subjected to forest harvesting and (*b*) density of roads in the Kakwa River basin. [Ripley et al. 2005]

evidence (e.g., Lee et al. 1997, see below) that no truly "safe" threshold road density exists, but rather negative impacts begin to accrue and be expressed with incursion of the first road segment. Ripley et al. (2005) further used the modeled negative relation between bull trout occurrence

and percentage of subbasin harvested (a primary driver of road construction) to forecast that forest harvesting over the next 20 years is projected to result in the local extirpation of bull trout from 24% to 43% of stream reaches that currently support the species in the basin.

- Similarly, bull trout redd numbers and changes in redd numbers with time were negatively correlated with density of logging roads in spawning tributary catchments in Montana's Swan River drainage (Baxter et al. 1999).

- U.S. Fish and Wildlife Service's Final Rule listing bull trout as threatened (USFWS 1999) states:

     A recent assessment of the interior Columbia Basin ecosystem revealed that increasing road densities were associated with declines in four non-anadromous salmonid species (bull trout, Yellowstone cutthroat trout, westslope cutthroat trout, and redband trout) within the Columbia River Basin, likely through a variety of factors associated with roads (Quigley & Arbelbide 1997). Bull trout were less likely to use highly roaded basins for spawning and rearing, and if present, were likely to be at lower population levels (Quigley and Arbelbide 1997). Quigley et al. (1996) demonstrated that when average road densities were between 0.4 to 1.1 km/km\2\ (0.7 and 1.7 mi/mi\2\) on USFS lands, the proportion of subwatersheds supporting "strong" populations of key salmonids dropped substantially. Higher road densities were associated with further declines.

- Lee et al. (1997) concluded, "Our [Interior Columbia Basin] results clearly show that increasing road densities and their attendant effects are associated with declines in the status of four non-anadromous salmonid species [bull trout, westslope cutthroat trout, Yellowstone cutthroat trout, and redband trout]. They are less likely to use highly roaded areas for spawning and rearing, and if found are less likely to be at strong population levels."

- Within colder subwatersheds, bull trout populations were reported as strong nearly seven times more frequently in those with less than 2.5 miles of road per square mile than those with more (Rieman et al. 1997, Table 5).

- Of five watershed integrity indicator variables used, the proportion of a subbasin composed of wilderness or roadless areas seemed most closely associated with subbasins having high integrity indices within the Interior Columbia basin; 81 percent of the subbasins classified as having the highest integrity had relatively large proportions of wilderness and roadless areas (>50 percent). Conversely, of subbasins with the lowest integrity, 89 percent had low proportions of roadless and wilderness areas, and 83 percent had relatively high proportions of at least moderate

road density (0.27 miles/square mile) (Gucinski et al. 2001, p. 8, citing Quigley et al. 1997).

- Lee et al. (1997) compared projected road densities against known aquatic conditions across the Interior Columbia basin and found that areas with estimated road densities of <0.06 km per square km (0.1 miles per square mile) were most generally associated with areas of low degradation and areas with estimated road densities of >0.43 km per square km (0.7 miles per square mile) were most generally associated with high degradation.

- Extensive habitat and population surveys on the Clearwater National Forest, Idaho, found that with few exceptions, native salmonid abundance was higher and exotic brook trout abundance lower or zero in unroaded versus managed landscapes (Huntington 1995). Differences were largest (often several-fold to an order of magnitude) and most consistent in the lower-gradient ("B" and "C") channel types, which are most sensitive to road and other management impacts, and were evident despite less-than-ideal stream habitat conditions in a large proportion of the stream segments in the unroaded landscapes, due to ongoing recovery from large fires within the past 50-150 years.

- Density of large wood (a crucial element of high quality aquatic habitat) in pools in tributaries to the Elk River, Oregon was negatively correlated with road density at intermediate ("network") spatial scales (Burnett et al. 2006). Road density was also negatively correlated with forest cover, which was likewise negatively correlated with large wood density, leading the authors to interpret the significant road density effect as an integrator or surrogate for impacts of the timber harvest associated with the road network.

- Frequency of large pools and all pools (crucial elements of aquatic habitat quality) declined with increasing road density in lower-gradient (<0.02) streams in the Interior Columbia River Basin (Lee et al. 1997).

- Thompson and Lee (2000) used existing data sets to model landscape-level attributes and snorkel count categories of spring-summer chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) parr (juveniles) in Idaho. Resulting models predicted that chinook salmon parr would be in low count categories within subwatersheds with >1 km·km^{-2} (1.6 miles per square mile) geometric mean road densities and/or <700 mm mean annual precipitation.

- Inventoried roadless areas provide or affect habitat for over 55% of the Threatened, Endangered, or Proposed-for-listing species found on or affected by National Forest lands, representing approximately 25% of all animal species and 13% of all plant species listed under the Endangered Species Act within the United States, and for over 65% of Forest Service-designated sensitive species (Brown & Archuleta 2000).

Besides the perennial problem of resources insufficient to the overall restoration need, this prioritization issue takes on greater importance in the context of recent

or current agency policies and legislative initiatives. Though intended to efficiently and/or collaboratively address multiple restoration objectives simultaneously, most existing policies/proposals risk the perverse outcome of directing restoration efforts or expenditures away from the locations of greatest need and most-certain benefit for aquatic/watershed restoration, especially in the absence of robust scientific sideboards circumscribing the decision space. For example, our reviews of recent projects and forest plans (corroborated by private testimony from Forest Service personnel) suggest that while Forest Service Region One's "Integrated Restoration Strategy" includes a high-profile aquatic/watershed component, in practice purported "forest health" and fire-risk concerns drive the planning process and determine locations of projects, with any aquatic/watershed restoration measures subordinated to and entirely dependent for support on those perceived terrestrial priorities. Urgently needed aquatic/watershed restoration is thus held captive to terrestrial considerations, and these terrestrial considerations are often of high public controversy and sometimes of dubious scientific validity.   By contrast, the scientific basis for and ecological and cost-effectiveness of aquatic/watershed restoration measures such as road decommissioning or stormproofing and fish-passage barrier removal are thoroughly documented, straightforward, and uncontroversial. Such watershed restoration work is urgently needed to meet acute policy and legal mandates of the National Forest Management Act, Clean Water Act, and Endangered Species Act. The mandates of these environmental laws, and public demand for clean water and healthy fisheries, will not be met if rational road impact reduction programs are subjugated to controversial fuels reduction and salvage timber sales. This programmatic linkage by management agencies hinders the ability of the agency to restore watersheds and remediate roads effectively, creates unnecessary spending inefficiencies that jeopardize aquatic resources, and clearly constitutes bad public policy.

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Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

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Abstract: *Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.*

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

Resumen: *Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y nutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-*

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tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-hoc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.

Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranka et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Saw-whet Owls and Eastern Screech Owls (*Aegolius acadicus and Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvilis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species.

In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the meridians of high-speed roads (Cowardin et al. 1985), making them population sinks.

Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas >200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbustorum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus*

leucopus; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore

metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter

plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hillslope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced

by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also $CaCl_2$, KCl, and $MgCl_2$, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods

(Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofiak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages

may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery management to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phythoptera lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlahan (1997) found that herptile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use patterns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and

a) Upland habitat alteration and fragmentation

b) Aquatic and riparian habitat alteration and fragmentation

c) Cumulative extent of habitat alteration and "hyperfragmentation"

Direct habitat impact (roads and cutting units)
Zone of indirect or off-site impact
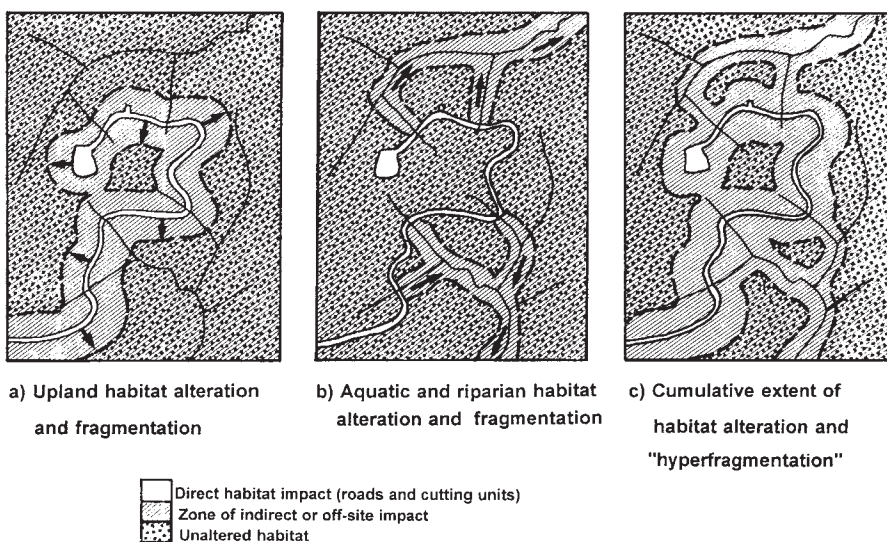Unaltered habitat

Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term hyperfragmentation *because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate predominant spatial vector of effects.*

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

Acknowledgments

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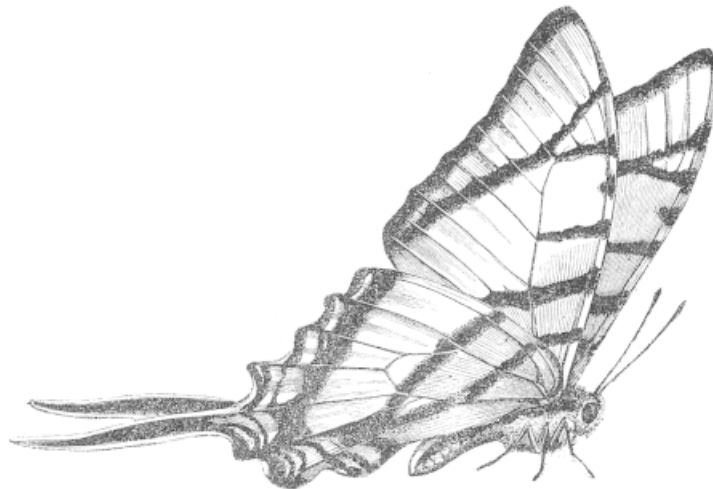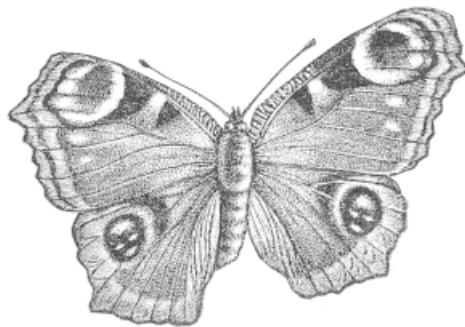
PATTERN AND PROCESS IN NORTHERN ROCKY MOUNTAIN HEADWATERS: ECOLOGICAL LINKAGES IN THE HEADWATERS OF THE CROWN OF THE CONTINENT[1]

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ABSTRACT: The Crown of the Continent is one of the premiere ecosystems in North America containing Waterton-Glacier International Peace Park, the Bob Marshall-Great Bear-Scapegoat Wilderness Complex in Montana, various Provincial Parks in British Columbia and Alberta, several national and state forest lands in the USA, and Crown Lands in Canada. The region is also the headwater source for three of the continent's great rivers: Columbia, Missouri and Saskatchewan that flow to the Pacific, Atlantic and Arctic Oceans, respectively. Headwaters originate in high elevation alpine environs characterized by high snow accumulations in winter and rainstorms in summer. Most headwaters of the region contain high quality waters with few ions in solution and extremely low nutrient concentrations. Alpine streams have few species of aquatic organisms; however, they often possess rare species and have hydrogeomorphic features that make them vulnerable to climatic change. Subalpine and valley bottom streams of the Crown of the Continent Ecosystem (CCE) flow through well forested watersheds. Along the elevation gradient, the streams and rivers of the CCE flow through series of confining and nonconfining valleys resulting in distinct canyon and floodplain reaches. The alluvial floodplains are characterized by high species diversity and bioproduction maintained by the hydrologic linkages of habitats. The streams and rivers of the CCE have low nutrient concentrations, but may be significantly affected by wildfire, various resource extraction activities, such as logging or mining and exurban encroachment. Wildfire has been shown to increase nutrient loading in streams, both during a fire and then following the fire for as much as 5 years. Logging practices increase nutrient loading and the algal productivity of stream periphyton. Logging and associated roads are also known to increase sediment transport into Crown of the Continent streams directly affecting spawning success of native trout. The CCE is one of the fastest growing regions in the USA because of the many recreational amenities of the region. And, while the region has many remarkably pristine headwater streams and receiving rivers, there are many pending threats to water quality and quantity. One of the most urgent threats comes from the coal and gas fields in the northern part of the Crown of the Continent, where coal deposits are proposed for mountain-top removal and open-pit mining operations. This will have significant effects on the waters of the region, its native plants and animals and quality of life of the people.

(KEY TERMS: Crown of the Continent; Northern Rocky Mountains; Canadian Rocky Mountains; alpine streams; subalpine streams; rivers nutrients; sediment; logging; mining.)

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INTRODUCTION

The Rocky Mountains in northern Montana and southern Alberta and British Columbia hold the geographic headwaters of a significant portion of the North American Continent. Indeed, within Glacier National Park resides a single spire, Triple Divide Peak, where three great river systems of the continent converge at the intersection of the Continental and Hudson Divides. Water flowing to the west enters the Columbia River basin (Pacific Ocean), waters flowing to the northeast flow into the Saskatchewan River basin (Arctic Ocean), and water flowing southeast enters the Missouri River basin (Atlantic Ocean). Thus, the montane landscape and its headwaters quite literally form the water tower of the continent. This region has been referred to as the Northern Continental Divide Ecosystem (Salwasser *et al.*, 1987), the Northern Rocky Mountain Province (Bailey, 1995), and the Crown of the Continent Ecosystem (Hayden, 1989). Although the first two names are most commonly used in scientific literature, they disregard the substantial portion of the contiguous montane system and headwaters in Canada. The term Crown of the Continent is more inclusive and representative of the importance of the region and is far and away the earliest title given recognizing the regional hydrologic and geographic uniqueness and appeared in an article written by George Bird Grinnell (1901) describing his travels in the region (Figure 1). Throughout the remainder of this paper we refer to the area as the Crown of the Continent Ecosystem (CCE).

The CCE is characterized by high heterogeneity of landscape and hydrology. To the east is the steppe of the Great Plains and the Rocky Mountain Front. Interior to the CCE are the belt series mountain ranges dominated by sedimentary geologic formations of mountains and valleys with elevation differentials extending from 1000msl at the valley floors to over 3000msl along the mountain peaks. The climate on the west slope of the Continental Divide is dominated by Pacific Maritime weather patterns flowing from west to east. Local climatic conditions are highly heterogeneous with some higher elevations receiving more than 2 m of snow water equivalent in winter. At the other extreme, some of the valley bottoms in the western portion of the CCE receive less than 20 cm of moisture per annum. Along the eastern slope of the Rocky Mountain Front the weather is highly variable, particularly in winter with cold, continental air masses flowing from northern Canada interrupted by warm air flow from the south, referred to as Chinook winds.

The core of the CCE is Waterton-Glacier International Peace Park, which holds a United Nations designation as an International Biosphere Reserve and World Heritage Site. Central to this designation is the role of aquatic biodiversity and the quality and quantity of water as it interacts with the mountain-valley landscape. Indeed, the distribution and abundance of biota and the way people use the landscape are closely interconnected to the region's headwaters. Some of the best evidence for climatic change globally is found here. The glaciers of Glacier National Park (GNP) have been shrinking rapidly since the founding of the park in 1910. A recent analysis estimated an ≈40% reduction in glacier volume since 1950 and simulation modeling has projected that the glaciers of GNP will be gone by 2050 (Hall and Fagre, 2003). This will have a significant effect on headwater hydrologic regimes and the organisms that are dependant on continuity of flow in alpine running water habitats (Hauer *et al.*, 1997).

The CCE is experiencing rapid growth in human population, particularly in the Flathead River basin in the western part of the Ecoregion. Natural wildness, recreation and scenic attributes, epitomized by Glacier National Park and Flathead Lake, are the long-term primary drivers of economic growth for the region. Water quality, the support of aquatic organisms, and the integrity of aquatic and riparian habitats are essential to maintaining the renewable goods and services (*sensu* Costanza *et al.*, 1991) that characterize the quality-of-life enjoyed by residents and visitors from around the world. The CCE is critically important to the biodiversity and ecological integrity of the entire continent. Indeed, the CCE holds one of the highest accumulations of diversity of plants and animals in North America (Stanford and Schindler, 2005), including the full array of native carnivores and ungulates. For example, valley bottoms and the river floodplains of the CCE are critical habitat for most of the large animals of the ecoregion, including several species listed as sensitive, threatened or endangered, including bull char, westslope cutthroat trout, wolves, grizzly bear, lynx, and wolverine.

The objectives of this review paper are to (1) introduce the importance of water resources in the CCE to continental scale biodiversity of complexity, (2) illustrate hydrogeomorphic, biogeochemical, and organismal linkages between CCE alpine, subalpine and valley bottom headwater streams and their coupling to water quality and quantity and regional biocomplexity, (3) present supporting studies that demonstrate the various sources and processes associated with both natural and man-caused disturbance and their effects within the CCE, and finally (4) discuss pending threats to headwaters that will likely affect the larger river systems that flow from this ecoregion, as well as direct impact to ecosystem integrity within the CCE itself.
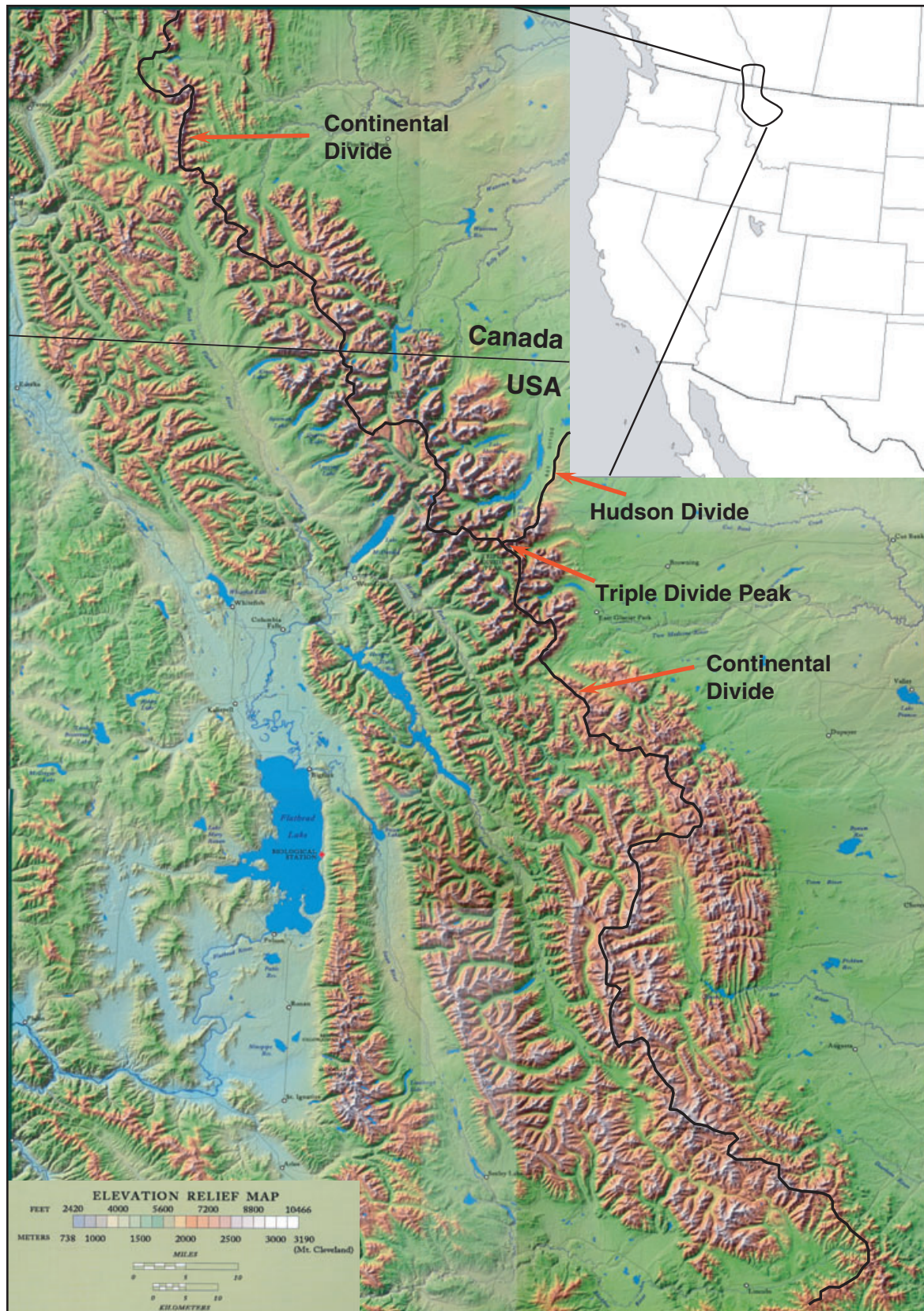
FIGURE 1. Map of the Crown of the Continent Ecosystem Illustrating Topographic
Relief and Major Federal, State, and Provincial Protected Lands in the USA and Canada.

HYDROLOGIC AND ECOLOGICAL LINKAGES IN THE CCE

Alpine Streams

Alpine streams throughout the world have varied hydrologic and biogeochemical characteristics, as well as variation in biota. Despite the worldwide distribution of alpine stream systems, studies of their biota and biogeochemistry are limited (Ward, 1994). There are three main types of alpine streams developed from descriptions in the European literature of the Alps; kryal, krenal and rhithral, each with distinct biotic and abiotic characteristics (Illies and Botosaneanu, 1963). Kryal streams are fed by year-round melt water directly from snowfields, icefields and glaciers and are characterized by high heterogeneity within and between streams of this type. Krenal streams arise as springbrooks hydrologically maintained by ground water. Krenal streams generally have relatively stable chemical, hydrological and thermal conditions. Rhithral streams are driven by seasonal snowmelt, and have wide temperature fluctuations, as well as diverse biota. Krenal streams in particular transition into rhithral streams as distance from the ground-water sources increase and waters coalesce from first order streams (*sensu* Strahler, 1964). Alpine streams often have high gradients with waters flowing over bedrock and cobble-boulder substrate, high dissolved oxygen levels, high variation in temperature regimes due to open canopies and summer solar radiation, and low nutrient concentrations.

Elgmork and Saether (1970) defined different zones of the streams based on genera of chironomids. The chironomid genus *Diamesa* dominated the upper, perennial snowmelt regions. The upper thermal limit of many of these species was 5°C. Again, based on chironomid community composition, Steffan (1971) defined the hypokryal and metakryal as distinct zones within kryal (glacial) streams in Scandinavia. Species assemblages within these zones were related to temperature. Hypokryal habitats were the most extreme in glacial streams, and supported very low numbers of individuals and species. Three species of *Diamesa* were the only invertebrates reported from the foot of glaciers in Sweden. These sites were isothermal, having mean temperatures from 0.5°C to 1.5°C, as well as very low daily temperature fluctuations.

Alpine streams of the CCE occur abundantly along the continental divide in Glacier and Waterton Parks. Waters of these alpine springbrooks were generally supplied by permanent snowfields or small icefields isolated behind mounds of colluvium. We found stream temperatures remaining at 0-0.5°C at the springhead and to vary less than 2°C within 0-10 m of the source. However, solar radiation in mid-summer can quickly elevate the temperature of these streams. We found mid-afternoon temperatures as high as 21°C in alpine streams within only a few hundred meters of their source. Although these streams can become quite warm during the day, often night temperatures at these sites ranged from 0-3°C. Thus, diel temperature flux in the alpine, at distances of a few hundred meters from the source, varied as much as 18°C.

Analyses of snow samples taken from 52 snow survey locations, mostly in the alpine and subalpine of Glacier Park, revealed very low nitrate concentration in snow water (mean = 4.36 $\mu g/l$; std. dev. = 1.31; Hauer *et al.*, 2003b). In a separate study, we found biologically available phosphorus (PO_4) concentrations to range between 0.5 and 0.7 $\mu g/l$ in kryal and krenal stream types (Figure 2a). In alpine streams with very low NO_3 concentrations, algal communities were frequently dominated by blue-green algae near the source. Diatoms replaced the blue-green algae even short distances downstream following incorporation of nitrogen into the stream system by the blue-green algae (Hauer and Giersch, 1999a).

Fauna of the alpine streams of the CCE is dominated by aquatic insects. Generally within 100 m of their source, krenal streams are dominated by several species of Simuliidae (black flies) and Heptageniidae (mayflies)(Hauer *et al.*, 2000). The stonefly, *Lednia tumana*, known only from alpine streams in Glacier Park, can be found in snowmelt streams and in springs with maximum summer afternoon temperatures exceeding 15°C. Generally, species assemblages increase in complexity downstream to include numerous mayfly nymphs from the families Heptageniidae and Ephemerellidae, several species of the predatory caddisfly larvae *Rhyacophila* spp., and the large predatory stonefly *Megarcys watertoni* (Hauer and Giersch, 1999b).

Both kryal and krenal streams reflect these low concentrations of NO_3 and PO_4 with the marked exception of the development of alpine fens, which form one of the most ecologically interesting associations in alpine streams. Fen development is under hydrogeomorphic control and occurs where ground water supplied by waters from a permanent snowfield are forced to the surface by bedrock (Figure 2b). Where the water source is diffuse, alpine vegetation grows and annually adds to an accumulation of undecomposed organic matter. The fen is characterized by permanently wet organic soils and a peat layer that is generally 10-20 cm thick. The fen, with its abundant alpine vegetation and peat, attracts populations of the heather vole, *Phenacomys intermedius*. The heather voles feed on the vegetation of the fen and

produce small burrows and food caches throughout the fen. They also produce latrine sites that are often placed in or near open water (Figure 2c). The deposits of frass and fecal pellets in the latrine sites

contribute significantly to the nitrogen and phosphorus loading of the krenal stream. We found NO_3 concentrations in the springheads associated with heather vole populations ranging from 100-250 $\mu g/l$ (i.e., 20-50 times the snow source concentrations) and PO_4 concentrations of 3-5 $\mu g/l$ (i.e., 5-10 times the snow source concentrations). These high concentrations of nutrients, especially NO_3, found in the krenal springheads, generally declined rapidly downstream. We found both NO_3 and PO_4 concentrations to decline 70-80% in $\approx$100 m of stream length. The fauna of these fen related krenal streams is also remarkable. The aquatic insect community of alpine fen streams is isolated to the caddisfly larvae *Allomyia bifosa*. This small caddisfly from the family Apataniidae, is extremely rare only known from high alpine kenal streams along the continental divide from Alberta and British Columbia to Montana. The *Allomyia* larvae feed on diatoms in the stenothermal krenal streams. We found these larvae to disappear from the stream when temperatures rise above 5°C. Thus, this very rare species appears to be restricted to krenal streams near the springhead with elevated NO_3 support of diatoms, but where temperatures remain near 0°C. This condition also appears to occur most readily where there is the presence of an alpine fen supporting a heather vole population.

The significance of these alpine aquatic environments, their low nutrient concentrations and the complex interactions described between hydrogeomorphic setting, terrestrial organisms such as heather voles, and very rare stream species, is manifold. First, these systems are the water towers of our continent. A large percentage of the water volume discharged each year from rivers such as the Columbia, Missouri, and Saskatchewan, or other river systems with origin in the Rocky Mountains, is generated as snow or rainfall within the mountain complex at higher elevations. Elevation and colder temperatures of the region extend the rate of snowmelt. Water, stored as snow, melts throughout the summer maintaining stream flow in the valleys and plains. This is critically important to maintaining both the ecological goods and services of the region (e.g., fisheries, wildlife, and recreation), but also agricultural uses and hydropower. Typically, the water quality is high with few nutrients and low concentrations of sediment. But, these aquatic systems are also fragile and highly vulnerable to climatic change as well as exploitation of the water resources. Although stream systems are connected through their dendritic network (Ward, 1997) the organisms of alpine segments may be isolated by thermal or habitat criteria making transfer from one stream to another difficult. This has led to regionally endemic species that are very vulnerable to extirpation. For example, the fen modified krenal

FIGURE 2. Photos of (a) Kryal and Krenal Streams Emerging From a Hanging Valley in Glacier National Park, (b) a Krenal Spring Stream With an Associated Alpine Fen, and (c) Fecal Pellets of Heather Voles (Phenacomys Intermedius) in "Latrine Sites" Deposited in the Krenal Stream.

streams are highly dependant on their hydrogeomorphic setting and are sustained by snowmelt over the summer. Late summer loss of the snowfield that supports the fen-krenal stream system, perhaps due to climatic change resulting in either less annual snow accumulation or earlier spring melting of the snow could lead to a loss of the wetland complex. This in turn could result in a radical change in state of the stream system from perennial to ephemeral (Hauer *et al.*, 1997).

Pristine Subalpine Streams

The subalpine of the CCE are highly variable, but tend to have similar unifying characteristics and species compositions. Hydrologically, these streams receive most of their flow from rain and snow deposited at high elevation of the alpine and within the subalpine zone of the mountain slopes. Abundant ground waters enter these streams following discharge into small springs along the toe of side slopes. Stream discharges in the CCE closely follow that of a snowmelt regime (Poff and Ward, 1989). In our study of McDonald Creek in Glacier National Park (Hauer *et al.*, 2000 and Hauer *et al.*2003b), we observed interannual variation in the magnitude and timing of maximum discharge, but this occurred each year of an 8-year study between mid-May and mid-June. Discharge typically increased >10 times the autumn base flow. Nutrient concentrations were always very low, but both nitrogen and phosphorus dynamics followed a positive, clock-wise hysteresis demonstrating an accumulation of materials poised to flux through the stream system at the onset of spring runoff (Figure 4). Over 90% of the total nitrogen flux from the McDonald Creek basin occurred as NO_3 with maximum concentrations approaching 450 $\mu g/l$, but minimum concentrations less than 100$\mu g/l$. These low concentrations predominate throughout the fall and winter base flow period and increase very rapidly at the onset of spring runoff. The rate of increase in NO_3 concentrations is significantly greater than the rate of increase in spring discharge. This suggests that nitrate is accumulated and concentrated in the ground water over the winter near the valley floor where the first snow melt that initiates the flood period occurs in the spring and discharges high NO_3 water from side slope aquifers into the stream. Nitrogen concentration decreases after the initial pulse in the early spring; and although discharge increases, primarily driven by high elevation snowmelt as the spring warming progresses, nitrogen concentration decreases. This is most likely the result of dilution of the ground water by melting snows from high elevation. Although we have no direct evidence, we

strongly suspect that the high concentration of *Alnus* spp. in avalanche chutes and high slope wetlands maybe play a significant role in the loading of NO_3 to subalpine shallow aquifers. Many studies have shown that soils directly surrounding stands of *Alnus* are rich in nitrogen allowing for increased production by neighboring species. Postgate (1978) showed how Alder communities can increase soil nitrogen as much as 100 kg-N/hectare/year through the mineralization of leaf litter alone. On a floodplain in the Alaskan interior, Alder communities are believed to have increased total soil nitrogen accumulation by a factor of four over a twenty year span (Walker, 1989).

We have observed a very different response in phosphorus concentration from that of nitrogen. During base flow soluble reactive phosphorus (SRP as PO_4) constitutes approximately 50% of the total phosphorus (TP) flux in McDonald Creek. However, during spring snowmelt TP increases in concentration in a linear fashion with increased discharge achieving maximum concentrations of $\approx 20\mu g/l$ (Figure 3). The majority of this phosphorus is associated with sediment particles, especially fine silts and clay (Ellis and Stanford, 1988). At peak discharge, biologically available SRP makes up less than 10% of the total phosphorus flux from the basin. Regardless of whether it is TP or SRP, phosphorus concentrations remain extremely low in McDonald Creek, which is typical of the undisturbed subalpine and valley bottom streams of the CCE.

In the pristine forest streams of the CCE, we observe very predictable temperature regimes closely
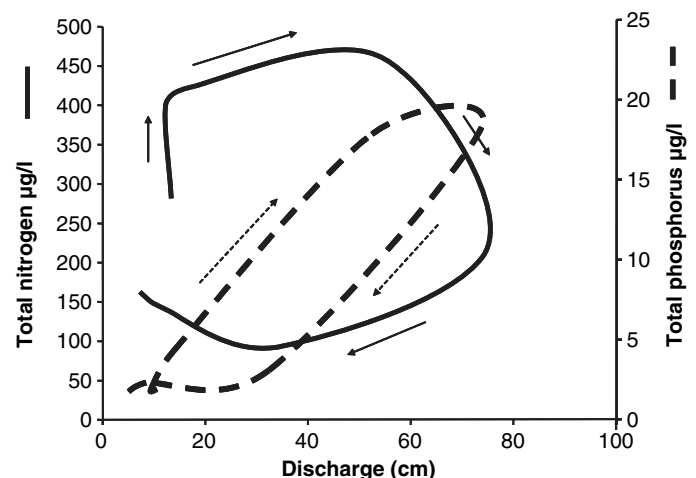

FIGURE 3. Regression of Total Nitrogen (Tn) and Total Phosphorus (Tp) Against Discharge in McDonald Creek, Glacier National Park. Hysteresis is caused by concentrations during the rising limb of the hydrograph being greater than concentrations during the falling limb of the hydrograph given the same discharge. Note that TN (mostly as NO_3) increases during early spring runoff at a greater rate than does TP (modified from Hauer *et al.* 2003).
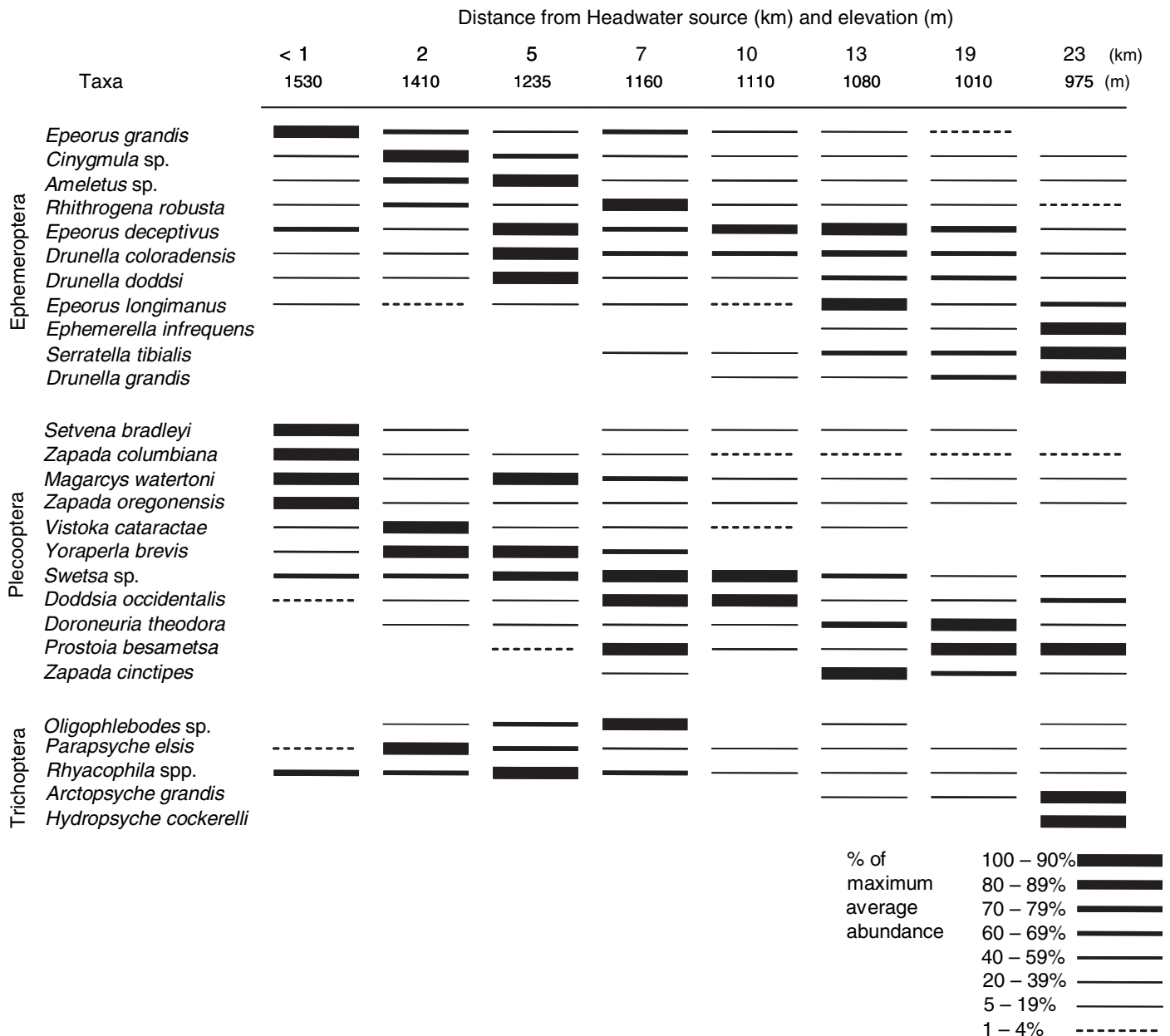
Distance from Headwater source (km) and elevation (m)

FIGURE 4. Distribution and Abundance of Commonly Occurring Benthic Macroinvertebrates Along the Elevation and Stream Gradient. Stream invertebrates are distributed along the elevation and longitudinal gradient within well-defined reaches having close correlation with maximum summer temperatures (modified from Hauer *et al.*, 2000).

correlated with elevation (Hauer *et al.*, 2000). This has a direct effect on the distribution of stream organisms and is particularly demonstrated among the stream benthic macroinvertebrate community. In this study (Hauer *et al.*, 2000), we quantitatively collected benthos samples at regularly scheduled intervals throughout the year over a several year period. Although we collected over 100 species of the three dominant orders of aquatic insects occurring commonly in CCE streams (i.e., Ephemeroptera, mayflies; Plecoptera, stoneflies; and Trichoptera,

caddisflies), we observed the 27 taxa illustrated in Figure 4 to occur in abundances that permit comparison of spatial distribution. We found an interesting phenomenon that can be directly explained by species specific energetics (Hall *et al.*, 1992). Taxa within the same order and possessing similar trophic relations had abundance patterns demonstrating statistically normalized distribution curves along the elevation (and thus temperature) gradient. For example, the net-spinning caddisfly *Parapsyche elsis* achieved maximum abundance in the upper reaches of
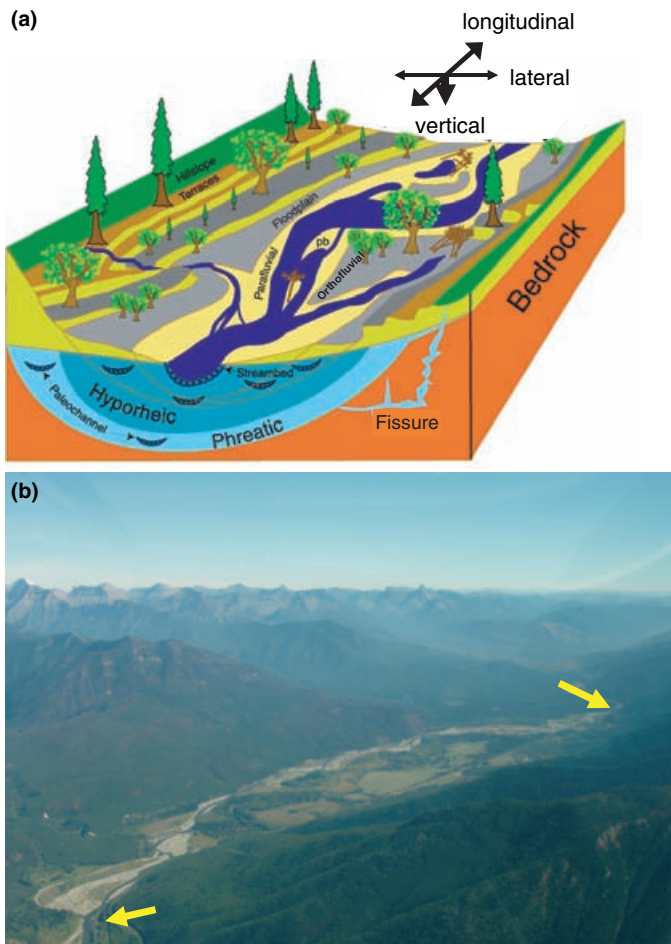
(a)

(b)

FIGURE 5. (a) Idealized View of the 3-D Structure of Alluvial the Floodplains of the CCE, Emphasizing Dynamic Longitudinal, Lateral, and Vertical Dimensions and Recruitment of Wood Debris. Arrows indicate ground- and surfacewater exchange (vertical), channel and flood plain (lateral) interactions, and upstream to downstream or longitudinal (horizontal) connectivity on the floodplain. The floodplain landscape contains a suite of structures produced by the legacy of cut and fill alluviation. The hyporheic zone is defined by penetration of river water into the alluvium. Phreatic ground water from the hillslope or other aquifers may underlie and/or be adjacent to the hyporheic zone. Alluvial aquifers usually have complex bed sediments with interstitial zones of preferential ground-water flow as illustrated by the buried river channel substrata (modified from Stanford et al., 2005). (b) Aerial view of the Nyack floodplain in the CCE. Yellow arrows mark the geomorphic knickpoints where the valley transitions from a canyon reach to the floodplain reach and then back to another canyon reach.

McDonald Creek, but were replaced in abundance by a similar net-spinning caddisfly, *Arctopsyche grandis* in the lower reaches of the creek, just above Lake McDonald. Physiological experiments in the laboratory have clearly demonstrated metabolic response of these species to change in temperature such that *P. elsis* larvae appear to be unable to sustain an energy and metabolic balance above 15°C and prefer reaches with temperatures having maximum summer temper-

atures <12°C whereas *A. grandis* larvae tolerate temperatures as high as 20°C and achieve maximum abundance in reaches with summer maximum temperatures between 17-19°C (Lowe and Hauer, 1999). Indeed, the vast majority of stream macroinvertebrates in the CCE have remarkably predictable distributions along the elevation and temperature gradient (Stanford et al., 1988, Hauer et al., 2000; Figure 4).

Valley Bottom Streams and Rivers

Valleys of the CCE were modified by Pleistocene alpine glaciers that carved through the landscape. Valley bottom, alluvial streams and rivers are characterized by broad and active alluvial floodplains, with highly complex physical and biological interactions between main river channels, surficial backwaters, springbrooks, and buried paleo-channel networks (Stanford and Ward, 1993; Hauer et al., 2003a,; Stanford et al., 2005). These complex interactions within and between habitats are driven by strong lateral and vertical flux of water and materials including flood-caused cut and fill alluviation, routing of river water and nutrients above and below ground, channel avulsion, and dynamics of large wood (Figure 6). The
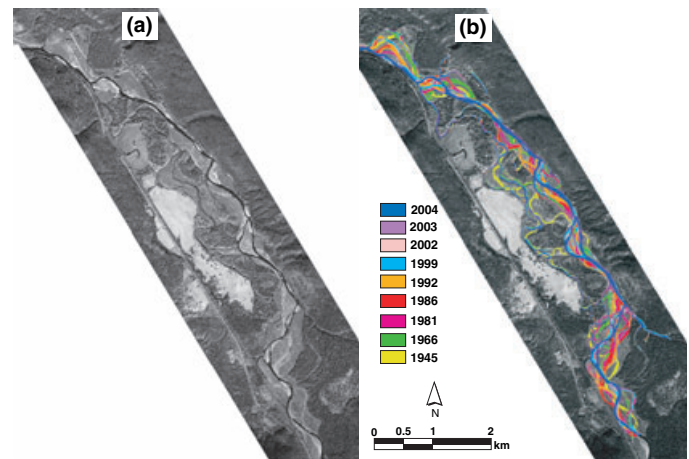
(a)　　　**(b)**

FIGURE 6. (a) Satellite Multi-Spectral Image of the Nyack Floodplain (Middle Flathead River, Montana 2004). The flood plain extends laterally to both valley walls. Much of the gallery forest of cottonwood and spruce has been cleared for hay farming. Owing to the porous nature of the valley bedsediments, a legacy of river deposition since glaciation, river water downwells into the alluvial aquifer beginning at the upstream knickpoint where the river becomes unconstrained. The downstream knickpoint defines entry into another canyon which impounds the alluvial aquifer allowing it to intersect the surface creating springbrooks and wetlands as water flows from the aquifer back into the river. (b). Here the position of the main channel during a sequence of years from 1945-2004 color coded to emphasize the dynamic nature of the river. Figure from Stanford et al. (2005).
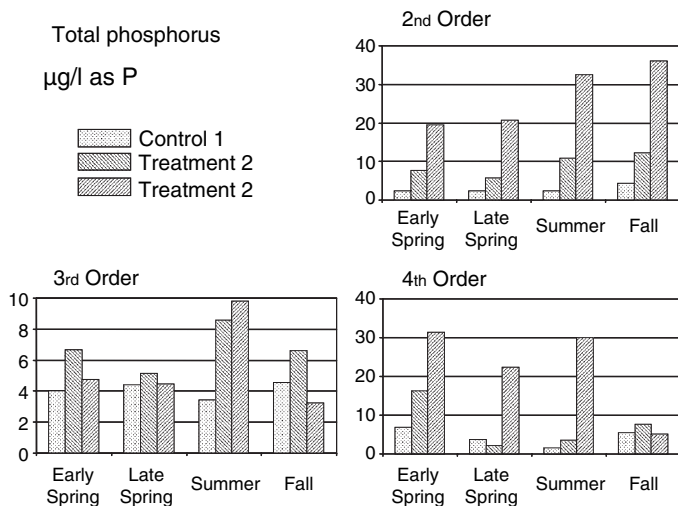
FIGURE 7. Total Phosphorus Concentrations of Paired Watershed Streams. Watershed groups are distributed across 2nd-, 3rd-, and 4th-order streams. Control streams flow from undisturbed watersheds. Treatment streams flow from watersheds with logging and associated roads (modified from Hauer and Blum, 1991).

strong forces are driven by the river hydrologic regime and sediment dynamics to form and maintain a complex, dynamic distribution of resource patches and associated biota: the shifting habitat mosaic (SHM; Stanford et al., 2005). These characteristics are critically important in maintaining water quality, bioproduction, and biodiversity of the river system. The SHM is maximized on expansive river floodplains producing inherently high biodiversity and biocomplexity. This is particularly well illustrated on the Nyack Floodplain of the Middle Fork of the Flathead River where over a 60 year interval river dynamics and the processes of cut and fill alluviation result in a shifting channel eroding old surfaces and creating new surfaces (Figure 7).

Floodplains composed of coarse sediments engaged in the processes embodied by the SHM are penetrated by river waters creating complex three-dimensional mosaics of surface and subsurface habitats (Stanford and Ward, 1988; Brunke and Gonser, 1997; Poole, 2002). Ground water-surface water interactions are critical characteristics of these streams and their floodplain corridors. Alluvial aquifer water returning to the surface is generally higher in NO_3 and PO_4 than surrounding surface flows, resulting in patches of high algal productivity (Bansak, 1998; Wyatt et al., 2006). In the river, hyporheic return flow also results in increased macroinvertebrate growth and productivity (Pepin and Hauer, 2002) and growth rates of riparian vegetation (Harner and Stanford, 2003). Native species of fish, particularly the salmonids (bull char, west slope cutthroat trout, mountain whitefish) focus on the complexity of flood-

plains and spawn in habitats dominated by extensive ground water-surface water interaction (Baxter and Hauer, 2000).

The riparian floodplains of montane alluvial rivers are extremely ecologically diverse. The river valley floodplains of the CCE have extremely high biodiversity, from riparian plant species and aquatic food webs (Stanford et al., 2005) to large carnivores (Demarchi et al., 2003). The continuity of these highly diverse components of the CCE landscape is highly dependant on hydrologic linkages and the high water quality associated with the geology as well as the pristine character of large areas of the CCE (Stanford and Ellis, 2002).

Disturbance to Streams of the CCE

Whether started by natural causes, such as lightening, or intentionally by the native peoples, wildfire has been an integral component of forests in the CCE for thousands of years. During the period from the 1920s to the 1990s fire suppression efforts contributed to significant accumulations of fuel and dramatically changed the population structure of the forest. When forests have burned, forest policy and post-fire activities have often contributed to, rather than ameliorated, the disturbance to soil, water and reforestation (Karr et al., 2004). Forest wildfires occur, almost universally, during extended periods of dry-hot weather in mid to late summer. During this period, stream discharge is generally at base flow and stream temperatures at near maximum for the annual cycle. Study of the effects of wildfire on stream systems in the CCE have shown that during the fire streams flowing through burning riparian forest receive elevated temperatures directly from radiant heat and temperatures may increase sharply as the fire passes through the stream corridor (Hauer and Spencer, 1998). Although we have seen dead resident cutthroat trout in depositional pools of fire affected streams, many fish survive the short duration of elevated temperatures by seeking thermal refugia in areas receiving hyporheic ground water (Spencer and Hauer, 1991). Likewise, there is strong evidence that macroinvertebrates also seek thermal refugia by crawling or borrowing into the interstitial space of the cobble substrata (Gangemi, 1991).

Phosphorus and nitrogen dynamics in streams during and following a wildfire are particularly interesting and play a significant role in nutrient loading of streams in the short term and downstream lakes in the longer term. During the fire, ash from the fire is carried into the air and settles on the water surface of the stream. Ash accumulates in backwater areas and sinks to the stream bottom where it is entrained

in the gravel substratum. The ash has high phosphorus content, but low nitrogen content. The phosphorus leaches from the ash particles and raises the concentration of soluble reactive phosphorus. In the CCE, studies have shown SRP to increase >200 times background levels during the fire as ash is loaded into the stream (Spencer and Hauer, 1991). As phosphorus is leached from the ash, phosphorus concentrations in the stream generally return to background levels within a few days. Although occurring because of the same fire event, fire related nitrogen enters streams through the dissolution of smoke gases into the water. Both NO_3 and NH_4 increase in concentration during a wildfire by as much as 50 times as smoke drifts across the water surface. Thus, unlike ash, the delivery of nitrogen compounds to a stream may be highly variable over time and spikes in nitrogen concentration may occur repeatedly as smoke is carried by winds that shift direction carrying smoke to or away from a particular stream. Studies have further shown that NO_3 sources of nitrogen are produced by well ventilated fires and NH_4 sources are produced when fires are poorly ventilated or have incomplete combustion, such as smoldering fires (Spencer and Hauer, 1991). Watersheds of the CCE are known to continue leaching phosphorus and nitrogen above background levels, particularly during spring snowmelt, for as much as 5 years after the fire (Hauer and Spencer, 1998). There are also significant problems associated with postfire management, particularly the unintended consequences to salvage logging on forested public lands throughout the western United States, such as increased road building and sediment loading into streams, hardening of stream banks, and introduction of exotic species (Bestcha *et al.* 2004).

Although forest logging practices have greatly improved as "best management practices" have been adopted by most of the federal and state forests, watershed studies in the CCE clearly show effects of logging and associated activities on stream water quality. A paired watershed study showed the effects of logging on nutrient dynamics and algal growth as a first-order ecological response to increased nutrient loading (Hauer and Blum, 1991). This study was conducted on 9 paired watersheds draining national forest lands of the Flathead National Forest within the USA of the CCE. Watersheds were paired into three groups of three streams each. One group was composed of second-order streams, one group of third-order streams, and the third group was composed of fourth-order streams. In each group there was one stream that drained a watershed with no timber management and no roads, the other two streams of each group drained watersheds with timber harvest and associated logging roads. The stream pairings, the watershed size, percentage of the watershed logged and the total distance of roads within each watershed are summarized in Table 1.

The study showed that soluble reactive phosphorus (SRP), nitrate (NO_3), total phosphorus (TP), and total nitrogen (TN) were all higher among streams flowing from watersheds with timber harvest and roads than streams flowing from undisturbed (control) watersheds (Table 1). Employing an ANOVA for repeated measures, the study found that although the relationship was significant for both SRP and NO_3, it was highly significant for TP (Figure 8) and TN (Figure 9). The ecological significance of this can be explained by the relationship between these highly labile forms of nutrients (SRP and NO_3) compared to the addition of more refractory forms of these nutrients (TP and TN) as they appear in particulate organic matter. The labile nutrients (SRP, NO_3) are generally transported distances measured in meters before they are taken up by periphyton in the process of stream nutrient spiraling (*sensu* Webster and Patten, 1979; Elwood *et al.*, 1983). Thus, both SRP and NO_3 are rapidly incorporated into stream algae before being re-released or semi-permanently bound in algal biomass (Mulholland *et al.*, 1985; Mulholland *et al.*, 2000). In contrast, TP and TN while including SRP and NO_3, include organically bound molecules, such as sloughed algae, that is transported by the stream.

TABLE 1. Watershed Groups, Areas, and Logging History of Nine Watershed Pairs. Streams Were Organized into Three Watershed Groups, Depending on Stream Order (2nd, 3rd and 4th Order). Within Each Watershed Group Was a Control Stream with No Logging and Two Streams with Logging in the Watershed (Modified from Hauer and Blum, 1991).

	Watershed	Watershed Area (ha)	Area Logged (ha)	% Logged
Watershed Group A	A1-Control	405	0.0	0.0
2nd Order	A2-Treatment	304	15.4	5.1
	A3-Treatment	435	127.9	29.4
Watershed Group B	B1-Control	2464	0.0	0.0
3rd Order	B2-Treatment	3010	461.9	15.3
	B3-Treatment	3494	338.9	9.7
Watershed Group C	C1-Control	3787	0.0	0.0
4th Order	C2-Treatment	4270	558.7	13.1
	C3-Treatment	4663	1127.9	24.2

Total nitrogen

µg/l as N
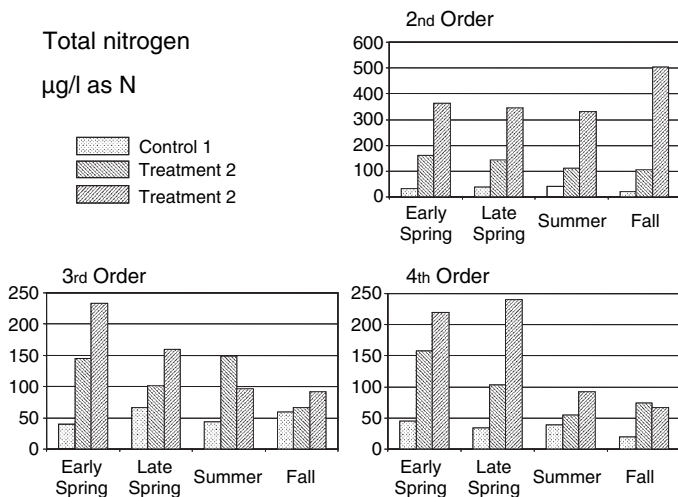
Control 1
Treatment 2
Treatment 2

FIGURE 8. Total Nitrogen Concentrations of Paired Watershed Streams. Watershed groups are distributed across 2nd-, 3rd-, and 4th-order streams. Control streams flow from undisturbed watersheds. Treatment streams flow from watersheds with logging and associated roads (modified from Hauer and Blum, 1991).
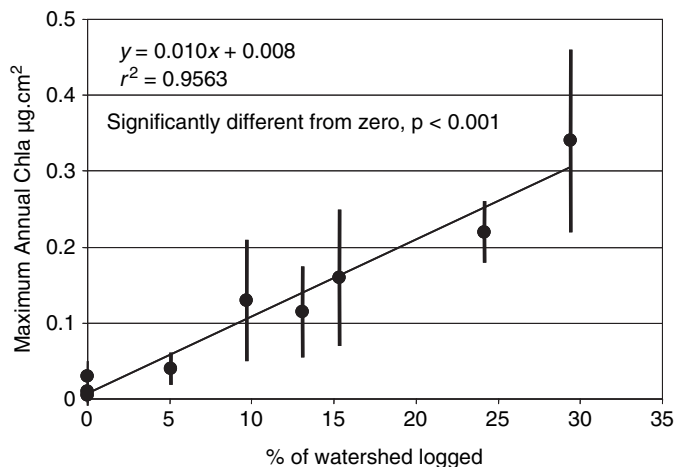

$y = 0.010x + 0.008$
$r^2 = 0.9563$

Significantly different from zero, p < 0.001

FIGURE 9. Mid-Summer Algal Biomass, Expressed as the Concentration of Chlorophyll α (μg cm^{-2}), as Affected by the Percentage of a Watershed That Has Been Logged (Modified from Hauer and Blum, 1991).

In this field experiment, much higher concentrations of TP and TN were observed in streams from logged (treatment) watersheds. These findings were corroborated by algal biomass and Chlorophyll α in each of the nine study streams (Hauer and Blum, 1991; Figure 9).

The results of this study clearly demonstrate the effect of logging on streams in the CCE. Streams of watersheds with logging have increased nutrient loading, first as SRP and NO_3, which is rapidly taken up by stream periphyton. This leads to increased algal growth that is directly correlated with the

quantity of logging within the watershed. The increased periphyton increases particulate organic matter in transport as the algal biomass is sloughed into the stream. We observed this as increased TP and TN in logged watershed streams. Other studies in the CCE have shown that increased sediment loading and an incorporation of fines into spawning gravel, especially during the summer and fall base flow period, has a dramatic effect on the success of spawning by bull trout (*Salvelinus confluentus*). Experiments have shown that as the percentage of fines increases from 20% to 40% there is >80% decrease in successful fry emergence (Weaver and Fraley, 1991).

While there are numerous sources of disturbance to CCE subalpine and valley bottom streams, logging and wildfire being two primary examples, exurban development along stream corridors is becoming an increasingly common occurrence. If recent trends continue, exurban encroachment into stream and river corridors will be a significant factor affecting ecological integrity of CCE headwaters and interact with other disturbance, both natural and human, in what frequently have unintended consequences. For example, as people build second homes for recreation in the headwater basins of the CCE, they frequently place a demand for fire protection on local, state and federal agencies, such as the US Forest Service. This, in turn, affects management decisions by the regulatory agencies as they make decisions prior to fire or manage post-fire landscapes (Beschta *et al.*, 2004; Karr *et al.*, 2004).

FUTURE AND IMPENDING THREATS

The Crown of the Continent Ecosystem is one of the fastest growing areas in the USA, particularly in the Flathead and Mission Valleys. Flathead County has grown over 25% in the past 10 years. The rate of building second homes on the private lands of the North Fork of the Flathead River has increased by nearly 10 fold in the past 20 years. Clearly, exurban development and encroachment into the headwater basins of the CCE will increase at an increasing rate over the next 10-20 years as the baby-boom generation begins to retire and seek the amenities of a clean and picturesque environment. However, there remain many other economic and resource extraction pressures on the headwater systems of the CCE.

During the 1970s high grade coal deposits were proposed for development in the Canadian portion of the North Fork of the Flathead River adjacent to the already active mining occurring in the Elk River Basin to the north. Considerable ecological work was done to evaluate North Fork water quality, biological

integrity, and air quality. The original mining proposal, referred to as the Cabin Creek Site, was denied in 1988 following evaluation by the International Joint Commission (IJC 1988). The IJC ruled that the potential threats to downstream water quality were unacceptable.

Integral to this decision by the IJC was the North Fork's status in the USA as the west boundary of Glacier National Park from the US – Canadian border to the North Fork's confluence with the Middle Fork, near West Glacier and Glacier National Park's designation as an International Biosphere Reserve by the United Nations. Also, the North Fork, designated a Wild and Scenic River in the USA, contributes approximately 25% of the total annual flow entering Flathead Lake, considered as one of the "Crown Jewels" of the US Northern Rockies EcoRegion.

Since the mid-1980's, various resource development plans in the Canadian North Fork (CNF) have appeared. Numerous haul and access roads have been built into the tributary drainages of the CNF. The Flathead Coalfields, located south of the Crowsnest Coalfields near Fernie, BC, are part of the Kootenay Group Outcrop. More recent resource exploration has identified new coal mining sites, potential for coalbed methane development, and possible oil and natural gas reserves.

Coal mining, coal-bed methane extraction, and oil and gas exploration require a vast network of roads, which have been shown as significant sources of silt and nutrients contributing to water pollution (Hauer and Blum, 1991), directly impact native fisheries (Baxter *et al.*, 1999), and have strongly negative consequences for large predators, such as grizzley bears (McLellan and Shackleton, 1988). Thus, there are highly likely negative impacts resulting from increased motorized access, noise and water quality changes associated with proposed coal or coal-bed methane extraction, and the additive relations to other forms of human mediated landscape change.

As is true of almost any protected area in the world, political boundaries in this region have little to do with ecological realities. The plants and animals in the CCE move freely across international, park or private ownership boundaries. Furthermore, Glacier National Park, by itself, is probably not large enough to support viable populations of many of its far-ranging predatory animals like wolves, grizzly bears, wolverine and mountain lions (Stanford and Schindler 2006).

While the headwaters of the Crown of the Continent have remained in remarkably good ecological condition, the pressures to exploit natural resources or develop lands near streams and rivers have direct impact on water quality and ecological integrity of these headwaters vitally important to human popula-

tions and ecological integrity of both the USA and Canada. As we seek to appropriately manage the waters of the CCE, we must keep in mind that human activities are pervasive and can have unintended consequences both for people and the biota throughout the region and beyond. It will also be imperative for future sound management of the CCE to recognize that neither the Ecoregion nor the various direct effects that have been the focus of this review are isolated from both human and environmental externalities. Coal and gas are part of an international market. People immigrate from one part of both the USA and Canada to another part. And finally, global climate change will have its own suite of effects that will in some cases alleviate some direct impacts and exacerbate others.

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Large woody debris in bull trout (*Salvelinus confluentus*) spawning streams of logged and wilderness watersheds in northwest Montana

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Abstract: We measured large woody debris (LWD) in 20 known bull trout (*Salvelinus confluentus*) spawning stream reaches from logged and wilderness watersheds in northwestern Montana. Mean bankfull width of stream reaches was 14.1 m ranging from 3.9 to 36.7 m. Streams were large enough to move LWD and form aggregates. We determined the characteristics of individual pieces of LWD that were interactive with the stream channel. Large, short pieces of LWD attached to the stream bank were the most likely to be positioned perpendicular to stream flow, while large, long pieces either tended to be parallel to the flow or, when attached, were most apt to extend across the channel thalweg. Observations indicated that the majority of pools were formed as scour pools by either very large LWD pieces that were perpendicular to the stream or multipiece LWD aggregates. Among reaches in wilderness watersheds, ratios of large to small LWD, attached to unattached LWD, and with and without rootwads were relatively consistent. However, among reaches with logging in the watershed, these ratios varied substantially. These results suggest that logging can alter the complex balance of delivery, storage, and transport of LWD in northern Rocky Mountain streams, and therefore, the likely substantive change in stream habitats.

Résumé : Nous avons mesuré les gros débris ligneux (GDL) dans 20 tronçons de cours d'eau servant de frayères à l'omble à tête plate dans des bassins exploités par l'industrie forestière et des bassins sauvages du nord-ouest du Montana. La largeur moyenne des tronçons à pleins bords était de 14,1 m, avec une fourchette de 3,9 m à 36,7 m. Les cours d'eau étaient assez larges pour que les GDL se déplacent et forment des agrégats. Nous avons déterminé les caractéristiques des morceaux de GDL qui interagissaient avec le chenal. Les morceaux gros et courts attachés à la berge étaient les plus susceptibles de se positionner perpendiculairement au courant, tandis que les morceaux gros et longs se plaçaient parallèlement au courant ou, s'ils étaient attachés, étaient les plus susceptibles de se placer en travers du thalweg du chenal. Les observations ont montré que la majorité des fosses sont le résultat de l'affouillement causé soit par de très gros morceaux de GDL perpendiculaires au courant, soit par des agrégats composés de plusieurs morceaux de GDL. Parmi les tronçons des bassins sauvages, les rapports des gros aux petits GDL, des GDL attachés aux GDL non attachés, des GDL avec et sans attaches racinaires, étaient relativement constants, alors qu'ils variaient considérablement parmi les tronçons des bassins soumis à l'exploitation forestière. Ces résultats permettent de penser que l'exploitation forestière peut altérer l'équilibre complexe de l'apport, de l'installation et du transport des GDL dans les cours d'eau du nord des Montagnes Rocheuses, et donc occasionner des modifications potentiellement importantes des habitats lotiques.

[Traduit par la Rédaction]

Introduction

Large woody debris (LWD) plays numerous roles in the structure and function of stream ecosystems (Gregory et al. 1991). Riparian forests contribute LWD to a channel network, directly affecting both large- and small-scale stream morphology, hydrologic processes, and stream biota (Abbe and Montgomery 1996; Bisson and Montgomery 1996). Large wood accumulations influence the dissipation of stream energy and thus the ability of the stream to transport material. For example, LWD has been associated with channel avulsion, floodplain formation, and island development (Abbe and Montgomery 1996; Nanson and Knighton 1996). LWD also plays an important role in localized modification of streambed morphology (Bisson et al. 1987; Ralph et al. 1994) and pool frequency and channel geometry (Beschta and Platts 1986; Fausch and Northcote 1992; Richmond and Fausch 1995). The orientation and position of LWD in streams affect storage of organic and inorganic matter (Bilby and Ward 1989; Nakamura and Swanson 1993). Likewise, wood serves as trophic support of stream biota by providing organic matter for stream invertebrates and substratum for attachment and growth (Angermeier and Karr 1984; Benke et al. 1985; Hauer and Benke 1991).

The factors that directly affect introduction, stability, or character of stream LWD have a potentially significant influence on native fish populations that utilize streams for spawning, rearing, or growth and completion of life histories

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(Andrus et al. 1988). Stream characteristics affected by LWD and its implications on salmonid populations have been the focus of numerous studies (e.g., Marcus et al. 1990; Ralph et al. 1994; Riley and Fausch 1995). A species of particular concern is the bull trout (*Salvelinus confluentus*), which has been in decline throughout the Pacific Northwest and was recently (1998) listed as a threatened species under the U.S Endangered Species Act. Numerous explanations for its decline have been offered, including habitat degradation (Fraley and Shepard 1989), overharvest (Rieman and McIntyre 1996), and displacement by exotic species (Leary et al. 1993).

Despite a generally ubiquitous trend of decline, the bull trout populations of the Flathead Basin in northwest Montana were considered relatively healthy, until recently. Strong spawning populations from Flathead Lake, Swan Lake, and Hungry Horse Reservoir have been an important part of the native fish fauna and an important sport fishery. In the past several years, however, the frequency of bull trout spawning in tributaries of the North and Middle forks of the Flathead River (i.e., the Flathead Lake population) has seriously declined (Rieman and Myers 1997). Overfishing, competitive interactions, predation of juveniles, food web alterations in Flathead Lake, and loss of habitat for spawning and rearing have all been suggested as causes for this decline. It is likely, however, that no single factor can be isolated as the overriding ecological bottleneck. Rather, all these factors influence the Flathead Lake population. For example, inundation of spawning gravels with fine sediments or changes in channel form and complexity may be major factors affecting the decline in bull trout spawning in the tributary drainages of the North and Middle forks of the Flathead River (Weaver and Fraley 1991). Low frequencies of spawning in some of the tributaries of the Swan River have been associated with the presence of logging roads (Baxter et al. 1999). Although the mechanisms that may be leading to the observed decline in bull trout are unclear, either on the landscape or in specific streams, hydrologic and vegetative changes associated with land use clearly play an important role. We suggest that a significant part of that role may be the result of change in the frequency, character, and distribution of in-stream LWD.

Although LWD plays an important role among streams in forested watersheds of the Pacific Northwest Coastal and Cascade Mountains (e.g., Nakamura and Swanson 1993; Ralph et al. 1994) and in the central Rocky Mountains (e.g., Fausch and Northcote 1992; Richmond and Fausch 1995), little information is available regarding the character or function of LWD in forested streams of the northern Rocky Mountains. The processes that have been documented among Washington and Oregon streams or streams in Colorado might not be seamlessly applicable in western Montana. Differences in climatic regime, landscape geomorphology, hydrologic regime, and the size, density, and longevity of dominant riparian species among these regions will have direct bearing on the interactive relationship between stream structure and function and LWD.

Regardless of the potential causes of bull trout population declines or the current cumulative effects impinging on the health and long-term viability of bull trout populations in western Montana, the maintenance of productive spawning and rearing habitat will be critical to the long-term sustainability or recovery of bull trout (see Fausch and Northcote 1992). As the recent changes in the food web of Flathead Lake come to some new quasi-equilibrium, with its cascading effects on higher trophic levels (Spencer et al. 1991), population restoration for bull trout will be strongly affected by reproductive success and juvenile survivorship. LWD may play a critical role in maintaining appropriate stream habitat and thus affect the long-term sustainability of bull trout populations in the Flathead Basin.

The purpose of this study is to describe the characteristics and selected functions of LWD among an array of historical bull trout spawning streams in the Flathead Basin. Although in several instances, redds occurred within a study reach, it was not our intention to specifically locate bull trout redds or covariation of redds and LWD. We selected streams from each of the four major tributaries in the drainage: the North and Middle forks of the Flathead River (Flathead Lake bull trout population), the South Fork of the Flathead River (Hungry Horse Reservoir population), and the Swan River drainage (Swan Lake population). We also chose streams that represented different types and levels of land use. Streams in the North Fork and Swan River include tributary drainages with extensive logging and riparian clearcuts. Streams in the Middle and South forks were within Glacier National Park or designated wilderness, respectively. The primary objectives of the research were to (*i*) characterize LWD in known bull trout spawning streams of the Flathead Basin, (*ii*) examine relationships of LWD size, position, and orientation across an array of stream sizes, (*iii*) examine the role of LWD in affecting local-scale bedform and stream morphology, and (*iv*) examine the potential effect of land use and (or) riparian logging on the size frequency structure, orientation, and decay relationships of LWD.

Materials and methods

Study area

This study was conducted in the Flathead Basin, a 22 241-km^2 drainage in northwestern Montana and southeastern British Columbia, along the west slope of the Continental Divide and within the belt series of the northern Rocky Mountains (Fig. 1). Sedimentary bedrock from the late Paleogene to the Proterozoic underlies the region and has been affected by low-grade metamorphism. These mountain ranges are part of the Rocky Mountain Belt Supergroup and consist of argillites, siltites, and carbonates with a maximum stratigraphic thickness of 5200 m (Whipple et al. 1984). Colluvium and glacial till mantle the heavily forested valleys. During the height of the last major glaciation, about 20 000 years ago, the Flathead Basin was covered by glacial ice. The main glacial advance flowed from the cordilleran ice sheet down the Rocky Mountain Trench. Smaller valley glaciers flowed from the Livingston, Whitefish, Swan, Flathead, and Mission ranges to merge along the valley floors, forming trunk glaciers as much as 1000 m thick. Alluvial valley segments of tributary drainages formed with faulting and local accumulations of valley fill from alluvial and glacial sources.

Twenty stream reaches were selected from a stratified random design for study from eight streams distributed around the basin (Fig. 1). All reaches were in third- or fourth-order segments. We consulted the Montana Department of Fish, Wildlife, and Parks

Fig. 1. Map of the Flathead Basin and northern Continental Divide region of northwest Montana showing the names of major river drainages and study stream reaches in unlogged wilderness watersheds (open circles), logged watersheds with unlogged riparian (encircled dots), and logged watersheds with logged riparian (solid circles).
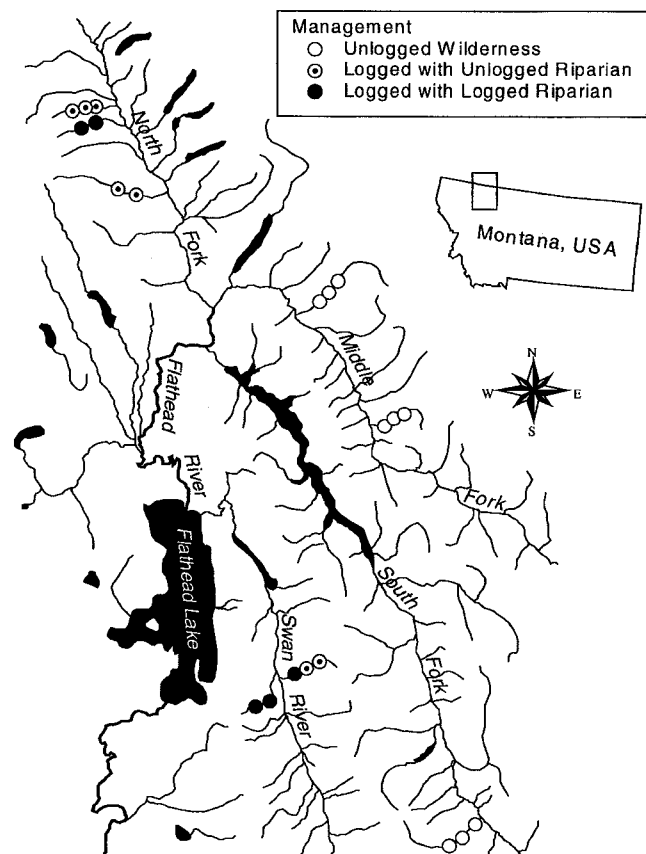
and selected study reaches within known bull trout spawning tributaries. We selected study streams within watersheds that had a land use history of either logging or wilderness management. Additionally, we selected specific study reaches within streams based on prevalent streamside management within the watershed. In some cases, as in Red Meadow Creek, the selected reaches flowed through riparian clearcuts, which occur commonly along that stream's length. Among other streams, such as Ole Creek in Glacier National Park, the riparian zone along the study reach was in an unaltered condition.

The substratum of each study reach was similar, generally composed of gravel and cobble, although occasionally, larger boulders (50–100 cm) were also present. The drainage area above the study reaches varied from 23 290 ha on Young's Creek to 1610 ha on Red Meadow Creek (Table 1).

Stream channel

Stream cross-sectional profiles, sinuosity, and gradient were measured at each stream reach using an Abney level, a Sonin® electronic distance measurer, and a leveling rod. Eleven transects (A–K) were taken across each stream reach at 10-m intervals covering a total reach length of 100 m. Each transect consisted of channel profiles measured perpendicular to the stream thalweg and to the top of the bankfull channel on both sides of the stream. Typically, 8–12 measures were taken to develop the cross-sectional profile at each transect. The profile data included all major breaks

in elevation, the wetted channel width, water depth at the thalweg (at the time of measure), and height of the average bankfull channel. The change in bed height and water depth between each transect profile was measured using the Abney level, electronic distance measurer, and leveling rod. The 10-m intervals between each transect were identified as a stream section and referenced to the downstream transect.

LWD measurements

Measures of LWD were made within each 10-m stream section between each transect. LWD was defined as logs $\geq$10 cm in diameter and $\geq$1 m in length. Although there are no standard criteria established as to the minimum size that constitutes LWD, the criteria used here are the same as used in research at other locations (Andrus et al. 1988; Fausch and Northcote 1992; Richmond and Fausch 1995). Each piece of wood meeting the LWD criteria was measured if any part occurred within or was suspended above the bankfull stream channel. The diameter was measured at each end of the LWD piece with a 1-m caliper. The length of each piece was measured with the electronic distance measurer if the length was >2 m or with the caliper for shorter pieces. Piece volume was calculated as a tapered cylinder (Lienkaemper and Swanson 1987). All large rootwads were considered LWD regardless of length. Stumped rootwads with a length <1 m were common among streams with logged riparian areas. Volume of rootwads was estimated by measuring the diameter of the root structure across the dominant mass as one end of the cylinder, the bole of the tree stump above the root structure as the other end of the cylinder, and the distance between these measurements as the tapered cylinder length. The position and orientation of LWD to the channel were determined for each LWD piece. Piece position was recorded as one of three possibilities: (*i*) no contact with either bank, (*ii*) contacting either the left or right bank, or (*iii*) contacting both banks. In addition to simply contacting a bank, many pieces were strongly "attached" to one or, rarely, both banks. We classified an LWD piece as being attached if either or both ends were anchored into the stream bank.

Orientation of LWD is known to affect stream flow and bed morphology (Robison and Beschta 1990). Likewise, stream power affects piece orientation because hydraulic forces move unattached ends in a downstream direction (Nakamura and Swanson 1994). Piece orientation was divided into three categories: (*i*) at an about 0° angle (parallel) to the channel, (*ii*) at an about 45° angle to the channel, and (*iii*) at an about 90° angle (perpendicular) to the channel. We also noted whether an LWD piece had a rootwad attached to the bole, since this plays an important function in the attachment, orientation, and distribution dynamics of the piece.

The relative age of each piece was assessed using a modification of the Grette (1985) decay classification procedure, which divided LWD into four decay classes: (1) bark and branches attached, (2) bark and branches missing; wood solid with evidence of decay restricted to the outer perimeter, (3) wood showing significant signs of decay to at least depths of 5–10 cm, and (4) wood soft and decayed nearly or completely to the center of the piece. We later combined categories 3 and 4 for our analysis because of the infrequency of observing type 4 decay class LWD. We believe that the scarcity of decay class 4 wood is due to the rapidity of final decay and disappearance once a piece undergoes a transition from decay class 3 to class 4.

Data analyses

We conducted a variety of statistical analyses including χ^2, correlation analysis, ANOVA, and MANOVA using the statistical analysis software SPSS for Windows by SPSS, Inc. We considered test results to be significant at $\alpha = 0.95$.

Table 1. River drainage, stream name, watershed area above study reaches, number of pieces in aggregates or not in aggregates, and other characteristics of LWD.

Flathead River drainage	Stream Name	Drainage area (ha)	Reach and logging condition	LWD aggregate (no.)	LWD nonaggregate (no.)	LWD volume (m³)	LWD attachment	
							Attached	Unattached
Middle Fork	Ole Creek	10 295	A[a]	0	13	8.8	5	8
			B[a]	18	11	7.4	17	12
			C[a]	0	32	30.8	7	25
	Nyack Creek	22 005	A[a]	0	7	0.4	1	6
			B[a]	0	5	3.0	2	3
North Fork	Red Meadow Creek	1 612	A[c]	10	41	35.9	35	16
			B[c]	53	70	73.3	95	28
	Whale Creek	9 836	A[b]	0	56	14.3	26	30
			B[b]	0	87	19.4	37	50
			C[b]	39	52	58.9	59	32
	Coal Creek	12 113	A[b]	51	72	33.3	57	66
			B[b]	11	25	19.8	19	17
South Fork	Young's Creek	23 289	A[a]	145	39	73.2	90	94
			B[a]	49	28	18.6	49	28
			C[a]	0	37	10.1	17	20
Swan River	Jim Creek	3 705	A[c]	71	46	65.2	72	45
			B[c]	0	46	10.9	35	11
	Goat Creek	5 602	A[b]	16	45	18.1	31	30
			B[b]	35	35	20.4	49	21
			C[c]	27	48	56.7	54	21

Note: Diameter class: 1 = 10–19 cm; 2 = 20–29 cm; 3 = 30–39 cm; 4 = 40 cm.
[a]Reach in unlogged wilderness watershed.
[b]Reach in logged watershed with unlogged riparian.
[c]Reach in logged watershed with logged riparian.

Results and discussion

General characteristics of study reaches

Mean (±SD) bankfull widths among all stream reaches combined were 14.2 ± 6.6 m with a range of 3.9–36.7 m across all transects. Study reaches were variable, both between and within streams. Stream gradients among all reaches were moderate (mean 1.0%, maximum 2.6%) but again highly variable. The thalweg bed elevation of some downstream transects was higher than that of upstream transects, clearly illustrating streambed complexity.

Five of the 20 study reaches had one or more side channels. In cases where side channels were present, there was always one dominant channel. The side channels were always small with only minor flow. Side channels in two stream reaches contained a high density of LWD and likely were abandoned main channels.

Thalweg stream depths across all transects ranged from a minimum of 0.15 m in Ole Creek reach A to a maximum of 1.33 m in Young's Creek reach C. An examination of the relationship between drainage area and stream depth showed a significantly, positive correlation ($p = 0.016$) with stream maximum depths; however, neither mean nor minimum stream depth was significantly correlated with basin size (Fig. 2).

General characterization of LWD

A total of 1320 pieces of LWD were counted and measured among all study reaches. The number of pieces and volume of LWD across all reaches were highly variable

(Table 1). For example, reach A on Young's Creek had 184 pieces, while, in contrast, reach B on Nyack Creek had only five pieces of LWD.

Across all stream reaches, the size of the LWD was also extremely variable. About 70% of all LWD was in the smaller two diameter classes (10–19 cm: >35%; 20–29 cm: >30%) (Fig. 3A) and >50% of the LWD was between 1 and 4 m in length (Fig. 3B). Size frequency of diameter measures and tree length measures demonstrated a decreasing exponential curve with increasing piece size. Together, <50% of the LWD across all stream reaches consisted of pieces >30 cm in diameter and >4 m in length. However, as in other studies (e.g., Abbe and Montgomery 1996), we found that the larger LWD pieces played the primary role in streambed configuration and the formation of aggregates (see data analysis below). LWD pieces that had been moved by the stream into large debris jams, or aggregates, often spanned the stream channel and were extremely stable, owing to their mass and configuration with the stream banks and the LWD pieces within the jam.

Other studies have found that LWD attachment to one or both banks and (or) the presence of the tree's rootwad are important factors influencing the stability (i.e., the resistance to being moved during flood) and orientation of the LWD piece (Beschta and Platts 1986; Richmond and Fausch 1995). Among nonaggregated LWD, we found attachment to one or both banks and the number of pieces that had rootwads to be highly variable, commensurate with the high variation in LWD occurrence between stream reaches (Table 1). However, we did find statistically significant relation-

0° by diameter class				45° by diameter class				90° by diameter class				Rootwad	
1	2	3	4	1	2	3	4	1	2	3	4	With	Without
1	0	1	0	2	3	1	4	1	0	0	0	6	7
4	3	0	1	4	3	2	3	4	2	1	2	2	27
4	6	3	4	3	4	1	1	1	1	0	4	7	25
2	0	0	0	3	1	0	0	0	0	0	0	0	7
2	1	1	0	0	0	0	0	0	0	0	1	1	4
2	4	5	4	3	3	2	4	3	10	3	8	9	42
3	7	1	4	5	18	9	12	8	15	13	28	8	115
13	19	3	1	10	2	2	2	4	0	0	0	1	55
19	14	6	3	18	13	6	1	2	3	2	0	0	87
13	14	14	5	11	13	3	1	5	7	0	5	17	74
33	20	3	4	17	17	6	6	10	6	1	0	4	119
7	2	2	3	5	2	0	1	5	4	3	2	2	34
16	16	8	5	43	29	20	9	12	10	5	9	27	157
11	7	2	1	20	9	3	10	4	4	2	3	15	62
6	4	0	4	9	4	4	0	3	2	0	1	5	32
9	8	2	3	19	19	8	8	7	14	9	11	18	99
7	3	0	2	13	7	1	2	5	0	3	2	2	44
6	7	1	2	6	2	2	1	9	13	4	8	8	53
15	5	3	3	9	7	1	4	7	9	1	6	6	64
4	5	2	4	7	3	4	8	9	9	4	16	20	55

ships between the orientation of the LWD piece, the attachment of the piece to the bank, and both the volume and the length of the LWD piece. Using χ^2 analysis, we found that LWD tends to be significantly shorter among those pieces that are perpendicular to the stream flow (orientation 90°) than among those that are parallel (orientation 0°) to stream flow (Table 2). This is likely due to longer pieces being subject to rotation around an anchor point, such as a bank attachment, during flooding when stream power and floatation of the LWD are at their highest (Nakamura and Swanson 1994). We found a similar significant relationship of increased LWD piece diameter associated with pieces that were perpendicular to the channel compared with those parallel to the channel (Table 2). We also observed that bank attachment often extended a considerable distance onto the bank and back into the riparian vegetation. These pieces were often the most stable and demonstrated resistance to change in orientation.

In addition to girth and length influencing stream LWD position, we also examined the affect of LWD attachment on orientation. A χ^2 analysis revealed that LWD pieces that were perpendicular to the current had a significantly higher frequency of bank attachment (Table 3). We found these features to be particularly important, since perpendicular pieces were the most interactive with the stream channel in that they were often most responsible for change in streambed morphology and complexity (see LWD influence on streambed morphology below). We also examined LWD wood decay (Table 1). We found that among all stream reaches, most

LWD was in decay class 2, i.e., most pieces had been stripped of their bark and branches and showed only the earliest signs of rotting at the surface. This finding has the following implications: (*i*) most of the wood has been in the stream for at least several years, long enough to loose the outer bark and limbs, but not so long as to enter advanced decay stages and (*ii*) the paucity of decay classes 3 and 4 suggests that once an LWD piece enters the latter stages of decay, decomposition processes occur rapidly. The latter stages of decay may be strongly enhanced during spring runoff as increased stream power causes decomposing logs to break apart. We did not conduct tests to directly determine the rate of LWD decomposition; however, based on our knowledge of aggregate accumulations at sites that we have visited regularly since the mid-1970's, we know that LWD can remain >20 years with no signs of surface decomposition. Thus, it appears that LWD probably remains in these streams for periods exceeding 50 years (sensu Andrus et al. 1988). To summarize, those pieces that were perpendicular to the flow tended to be attached to the stream bank, large in diameter, and short. This finding corroborates Nakamura and Swanson (1994).

LWD influence on streambed morphology

An important feature of stream habitat structure is the development and stability of streambed morphology. Streams that alternate between riffles, pools, and runs provide complex habitats that support high biodiversity, biomass, and secondary production of aquatic insects and fish. Complex

Fig. 2. Maximum, mean, and minimum thalweg depths among all transects for each stream reach regressed against the drainage area of each watershed above the study area. The maximum thalweg depth to basin area correlation coefficient ($r = 0.51$) is significant at the 0.05 level. Correlations between mean and minimum thalweg depths and basin area were nonsignificant.

Fig. 3. Percentage of LWD in each of (A) eight bole diameter classes and (B) 11 length classes.
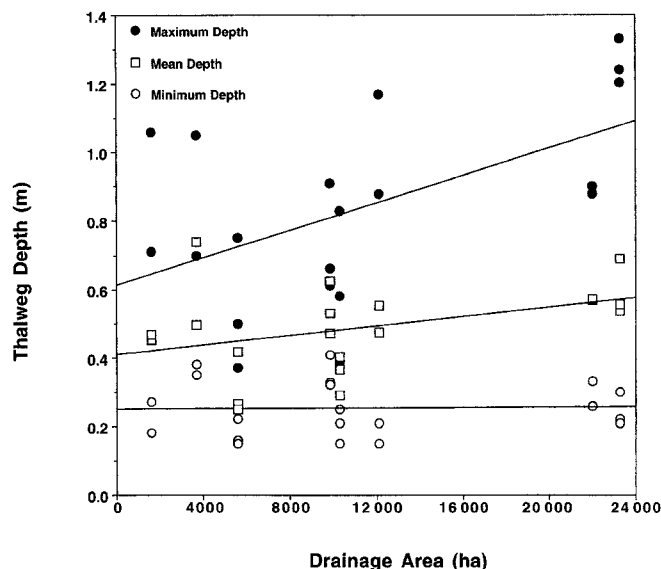
variation in stream habitat and streambed morphology is frequently required for different species to coexist (sensu Connell 1980).

Using correlation analysis, we examined the role of LWD and its influence on streambed morphology. We found that as the number of pieces of LWD and the volume of LWD increased within a stream section, there was a corresponding increase in the bedslope of the section immediately downstream (Fig. 4). The steepest bedslopes were all associated with upstream aggregates, large snags with rootwads, or large-diameter LWD oriented perpendicular to the stream thalweg. Each of these LWD structures performs important bed-forming functions, e.g., the retention of gravel on the upstream side of the structure and (or) the focus of stream flow and thus stream power and scour on the downstream bed material forming pools. Both of these factors lead to the aggradation of upstream gravel and cobble and the downstream degradation of bed material. These correlations between increased LWD piece frequency and volume and bedslope underscore the importance of LWD aggregates in stabilizing bedload, capturing gravel, and promoting pool formation.

Land use influence on LWD

Three of the eight watersheds (eight of 20 study reaches) examined were located within Glacier Park or the Bob Marshall Wilderness. These three watersheds are managed as wilderness and have never been logged or roaded. The other five watersheds are in the North Fork or the Swan River drainages and flow through lands managed for multiple use, but primarily for timber harvest.

We found a tight correlation ($r = 0.99$) between the frequency of large LWD (≥ 30 cm in diameter) and the frequency of small LWD (<30 cm in diameter) among the
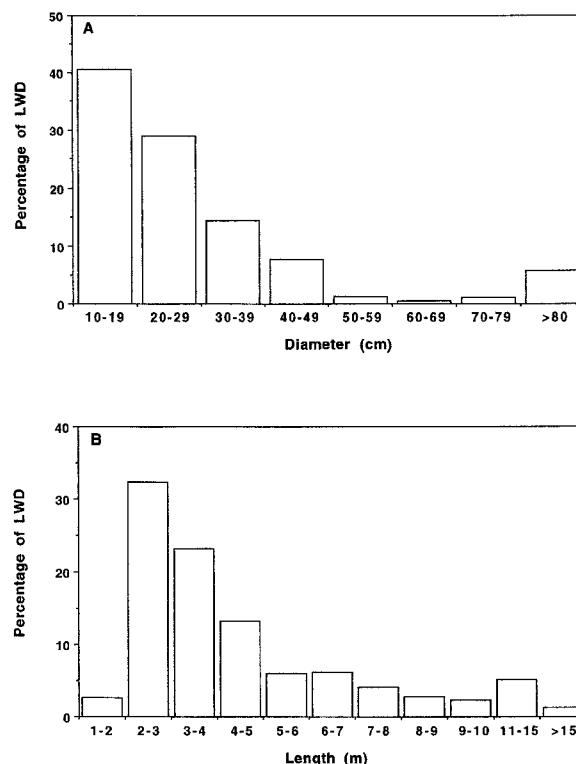
reaches draining wilderness areas (Fig. 5). In contrast, among reaches in watersheds with upstream logging, the large to small LWD relationship was poorly correlated ($r = 0.18$). These data suggest that even though variation in number of pieces of LWD among stream reaches may be high, there is a consistent and highly predictable relationship between the frequency of large-diameter trees and small-diameter trees in the LWD pool in wilderness watersheds that was not present in logged watersheds. In addition to the cross-watershed comparison of LWD size ratios, we further compared streams flowing through logged riparian zones with those flowing through unlogged riparian zones, but in logged watersheds. Among the logged watersheds, we found that streams flowing through logged riparian zones tended to have a higher large LWD to small LWD ratio than streams flowing from wilderness areas, while streams flowing from logged watersheds, but with unlogged riparian zones, usually had smaller ratios (Fig. 5).

We also examined the relationship of attachment of LWD to the stream bank. Again, we found that among wilderness watersheds, there was a relatively tight correlation ($r = 0.94$) between the frequency of attached LWD and the frequency of unattached LWD and a poorly correlated relationship ($r = 0.30$) among logged watersheds (Fig. 6). Additionally, we examined the relationship between the frequency of LWD pieces with rootwads and the frequency of those without rootwads. Again, among reaches in wilderness watersheds, there was a high correlation ($r = 0.96$) between LWD pieces with rootwads and those without rootwads, but among logged watersheds, this relationship was poorly correlated ($r = 0.13$) (Fig. 7).

Table 2. Chi square analysis of length and bole diameter versus attachment and orientation characteristics of nonaggregate LWD among all stream study reaches.

LWD characteristic	Attachment characteristic			Orientation characteristic			
	Attached	Unattached	Pearson χ^2	0°	45°	90°	Pearson χ^2
Length <4 m	219	155	0.05 (p = 0.82)	108	150	116	38.0 (p < 0.00)
Length ≥4 m	184	135		153	121	45	
Diameter <30 cm	236	232	35.4 (p < 0.00)	190	191	87	17.7 (p < 0.00)
Diameter ≥30 cm	167	58		71	80	74	

Table 3. Chi square analysis of attachment and orientation characteristics of nonaggregate LWD among all stream study reaches.

Attachment characteristic	Orientation characteristic			
	0°	45°	90°	Pearson χ^2
Attached	127	156	120	27.5 (p < 0.00)
Unattached	134	115	41	

Among all watersheds, there was high variance in the frequency of LWD. Furthermore, LWD is not evenly distributed at the stream reach (100 m) spatial scale. However, the ratio of large to small LWD, the ratio of attached to unattached LWD, and the ratio of LWD with and without rootwads were relatively consistent across stream reaches in wilderness areas. However, among stream reaches in logged watersheds, these relationships were highly variable. These data suggest that logging or associated land use activities within a watershed may result in an alteration in the balance of delivery, storage, and transport of stream LWD, which in turn would have strong implications regarding effects on material transport and stream habitats.

It would require additional, focused study to determine the cause and effect relationship between size, attachment, and rootwad frequencies of stream LWD and specific logging practices. However, regardless of whether increased variance in size frequency is the result of direct actions that alter LWD input to the stream (e.g., cutting of large-diameter riparian trees) or indirect forces (e.g., postlogging blowdown), they may contribute to LWD characteristics that depart from relationships among streams in unlogged watersheds. Such departures may result in substantive habitat alteration and adverse effects on species dependent on habitats affected by stream LWD structure and function, such as pool size and frequency, surface/ground water exchange, and complex channel morphology.

Implications for watershed and streamside management

We found a close association between LWD and streambed morphology. For example, the steepest bedslopes were all associated with upstream aggregates of LWD. Among nonaggregated LWD, we found large pieces attached to stream banks and oriented perpendicular to the thalweg to be more closely associated with pool formation than parallel or unattached pieces. Among LWD pieces that were oriented perpendicular to stream flow and crossed the stream thalweg, there was a statistically significant higher frequency of long pieces (i.e., ≥4 m in length), a nearly significant proportion of large pieces (i.e., ≥30 cm in diameter),

Fig. 4. (A) Number of LWD pieces and (B) volume of LWD in the upstream 10-m stream section and the corresponding downstream bedslope.
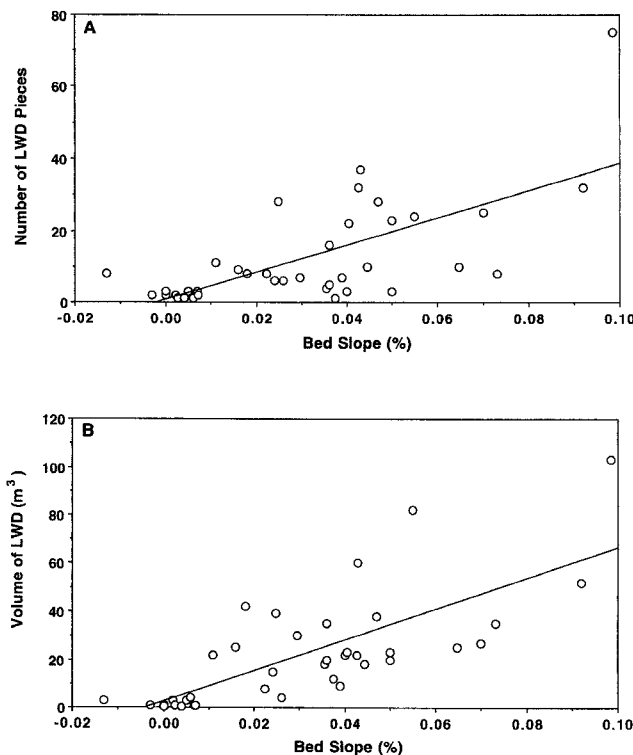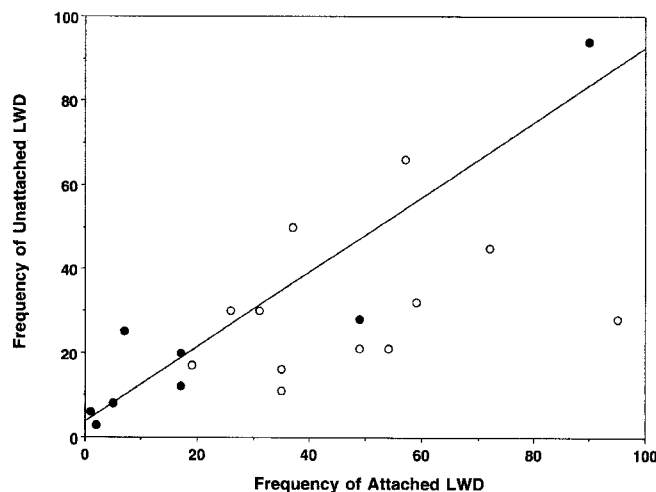

and a statistically significant higher frequency of LWD pieces attached to the stream bank (Table 4). These field observations suggest that LWD pieces that are perpendicular to the stream channel and engage the stream thalweg are the primary influence promoting pool formation. Field measurements further indicate that of the perpendicular LWD pieces, large-diameter pieces that are long and attached to the stream bank are the most stable (e.g., best able to resist reorientation and movement once in the channel). Grette (1985) and Richmond and Fausch (1995) also reported a significant positive relationship between LWD and the abundance of pools, as well as the importance of relatively few, stable LWD pieces that accounted for most of the pool formation.

Wohl et al. (1993) reported that stream depth, gradient, stream power, and the resistance of bed and bank materials to erosion were important determinants of pool size. We observed a similar relationship in which the streams of the larger drainages had the deepest pools, even though drainage size had no significant effect on mean or minimum thalweg

Fig. 5. Frequency of large-diameter (≤30 cm) versus small-diameter (<30 cm) LWD among study stream reaches in wilderness watersheds (solid circles) and in logged watersheds (open circles). Arrows denote study stream reaches with logged riparian areas. The trend line is for wilderness watersheds. Correlation coefficients are given in the text.
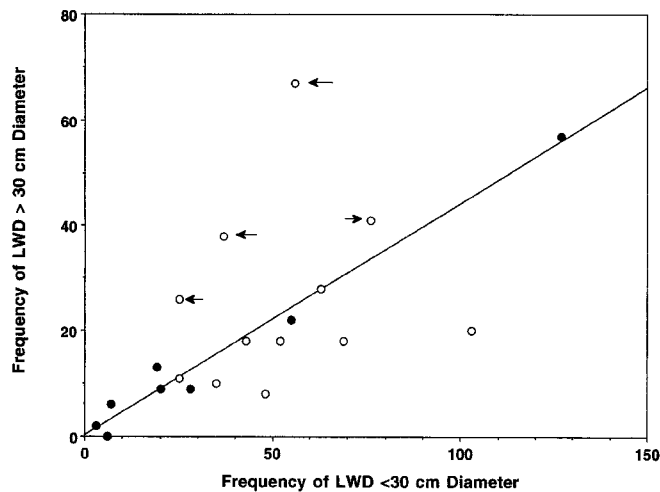

Fig. 6. Frequency of unattached versus attached LWD among study stream reaches in wilderness watersheds (solid circles) and in logged watersheds (open circles). The trend line is for wilderness watersheds. Correlation coefficients are given in the text.

Fig. 7. Frequency of LWD with rootwad versus without rootwad among study stream reaches in wilderness watersheds (solid circles) and in logged watersheds (open circles). The trend line is for wilderness watersheds. Correlation coefficients are given in the text.
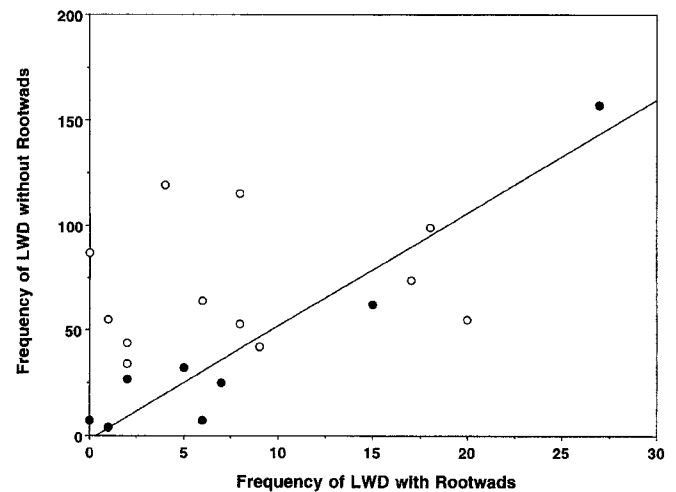
Table 4. Chi square analysis of length, bole diameter, and attachment characteristics of nonaggregate LWD crossing the stream channel and engaging the stream thalweg versus LWD within the bankfull channel but not engaging the stream thalweg.

| | Crossing characteristic | | |
| | Across thalweg | Not across thalweg | |
LWD characteristic			Pearson χ^2
Length <4 m	40	321	6.64 ($p = 0.01$)
Length ≥4 m	56	254	
Diameter <30 cm	57	396	3.38 ($p = 0.07$)
Diameter ≥30 cm	39	179	
Attached	66	324	5.20 ($p = 0.02$)
Unattached	30	251	

depth. Other researchers have suggested that for large streams and rivers, LWD generally has a limited effect on gradient, stream power, maximum stream width, and maximum bankfull depth (Andrus et al. 1988; Evans et al. 1993). Our results support this suggestion, since within the largest watershed streams, such as Young's Creek, pool-forming LWD pieces occurred almost exclusively as aggregates (Table 1). In other words, as a stream gets larger, exemplified by Young's Creek in our study, stream power becomes sufficient to move virtually all wood that enters the channel. However, this does not mean that as stream size increases, LWD becomes of little consequence but rather that the role of LWD may change as aggregates interact with the dynam-

ics of flood waters affecting anabranching and (or) avulsion behavior (e.g., Nanson and Knighton 1996).

Robison and Beschta (1990) and Richmond and Fausch (1995) showed that changing relationships between LWD and stream flow influenced pool types and that the majority of pools were formed by LWD spanning the channel perpendicular to flow. Richmond and Fausch (1995) found plunge and dammed pools to be the most prevalent pool type in the small subalpine streams of Colorado. Bilby and Ward (1989) found a similar pool type in smaller streams (<7 m wide) in southwestern Washington, but mainly scour pools in large streams (Bilby and Ward 1991). We observed similar situations among streams in the Flathead Basin where pools in the smaller streams (e.g., Goat Creek, Red Meadow Creek) were primarily associated with plunging or dammed water around LWD and with scour pools around aggregates in the largest streams (e.g., Young's Creek, Coal Creek).

In forested watersheds, LWD is an essential component in the formation of stream morphology and provides habitat for aquatic insects and fish. However, the relationship between stream size and power and the position and role played by LWD in the modification of bedform and channel develop-

ment is a changing one. It is apparent from this study that large-diameter, shorter pieces of LWD attached to the stream bank have a higher frequency of perpendicular orientation and that larger, longer pieces attached to the bank tend to interact with the channel, as represented by those logs that cross the thalweg. Thus, a greater degree of pool-forming interaction with stream flows is represented by large, long pieces of LWD attached to the stream bank. Likewise, as the stream size increases, a concurrent increase in the size of LWD comprising an aggregate is needed to remain stable and interactive with the channel. Thus, the interaction of stream power, bed characteristics, and LWD piece diameter, length, and position largely determines the structure and function of stream LWD. The distribution of LWD among size classes, and attachment and orientation categories appears relatively consistent across streams in unlogged watersheds but becomes less predictable in streams that have been influenced by logging. A detailed investigation into the specifics of various logging histories would be necessary to determine how specific site prescriptions affect the outcome of LWD relationships associated with forest streams.

The implications of this study for forest managers are twofold: (*i*) with riparian logging comes increased unpredictability in the frequency of size, attachment, and stability of the LWD and (*ii*) maintaining the appropriate ratios of size frequency, orientation, and bank attachment, as well as rate of delivery, storage, and transport of LWD to streams, is essential to maintaining historic LWD characteristics and dynamics. Our data suggest that exclusion of logging from riparian zones may be necessary to maintain natural stream morphology and habitat features. Likewise, careful upland management is also necessary to prevent cumulative effects that result in altered water flow regimes and sediment delivery regimes. While not specifically evaluated in this study, in general, it appears that patterns of upland logging over space *and* time may have cumulative effects that could additionally alter the balance of LWD delivery, storage, and transport in fluvial systems. These issues will be critical for forest managers attempting to prevent future detrimental environmental change or setting restoration goals for degraded bull trout spawning streams (cf. Reeves et al. 1991).

Acknowledgements

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